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Abstract

We provide a synopsis of ~60 million years of life history in Neotropical lowlands, based on a comprehensive survey of the Cenozoic deposits along the Quebrada Cachiyacu near Contamana in Peruvian Amazonia. The 34 fossil-bearing localities identified have yielded a diversity of fossil remains, including vertebrates, mollusks, arthropods, plant fossils, and microorganisms, ranging from the early Paleocene up to the late Miocene-?Pliocene (> 20 successive levels). This Cenozoic series includes the base of the Huchpayacu Formation (Fm.; early Paleocene; lacustrine/fluvial environments; charophyte-dominated assemblage), the Pozo Fm. (middle + ?late Eocene; marine then freshwater environments; most diversified biomes), and complete sections for the Chambira Fm. (late Oligocene–late early Miocene; freshwater environments; vertebrate-dominated faunas), the Pebas Fm. (late early to early late Miocene; freshwater environments with an increasing marine influence; excellent fossil record), and Ipururo Fm. (late Miocene–?Pliocene; fully fluvial environments; virtually no fossils preserved). At least 485 fossil species are recognized in the Contamana area (~250 'plants', ~212 animals, and 23 foraminifera). Based on taxonomic lists from each stratigraphic interval, high-level taxonomic diversity remained fairly constant throughout the middle Eocene-Miocene interval (8-12 classes), ordinal diversity fluctuated to a greater degree, and family/species diversity generally declined, with a drastic drop in the early Miocene. The Paleocene–?Pliocene fossil assemblages from Contamana attest at least to four biogeographic histories inherited from (*i*) Mesozoic Gondwanan times, (*ii*) the Panamerican realm prior to (*iii*) the time of South America's Cenozoic "splendid isolation", and (*iv*) Neotropical ecosystems in the Americas. No direct evidence of any North American terrestrial immigrant has yet been recognized in the Miocene record at Contamana.

Keywords

Fossil record; Paleobiology; Stratigraphy; Paleogeography; South America

Contents

The heavy vegetation in the jungles of eastern Peru conceals rock exposures; travel is possible only along trails; the best and only place to study the geology is along stream beds.

Bernhard Kummel (1948: 1221)

1. Introduction

1.1. Context

The Cenozoic fossil record of northern (tropical-equatorial) South America, particularly the Paleogene interval, consists almost exclusively of small numbers of specimens from scattered outcrops with generally poor age constraints (for a review, see Hoorn & Wesselingh, 2010; Hoorn et al., 2010a). In contrast to the Patagonian steppe or Andean highlands (see Flynn et al., 2012), intense vegetation cover, severe surface weathering, and seasonal flooding in Amazonia widely hamper access to extensive exploitable outcrops.

The first fossils reported from Amazonia were Miocene mollusks from Pebas in Eastern Peru (Gabb, 1869; Woodward, 1871), a small village east of Iquitos, Loreto Department (Fig. 1A) which subsequently gave its name to both a Miocene formation and the gigantic corresponding megawetlands system (see Hoorn et al., 2010b for a review). Subsequently, blue clays and lignite seams from this Miocene formation were extensively investigated for pollen (e.g., Hoorn, 1993, 1994), fish (Monsch, 1998), and mollusks (e.g., Wesselingh et al., 2002, 2006; Wesselingh & Ramos, 2010). The first fossil insects and mites from western Amazonia were uncovered in amber fragments originating from a late middle Miocene lignite level of the Iquitos area (Antoine et al., 2006; Petrulevičius et al., 2011; Perrichot et al., 2014). More recently, a species-rich crocodylomorph assemblage (seven species, including

three new taxa of shell-crushing caimans) was described from the same seam (Salas-Gismondi et al., 2014, 2015).

Very few descriptions of fossil vertebrates from other areas of Amazonian lowlands in Peru were published before the 1980s (Anthony, 1924; Patterson, 1942; Spillman, 1949; Willard, 1966; Buffetaut & Hoffstetter, 1977). By contrast, many field campaigns were organized in the 1980s and 1990s to search for Neogene and Pleistocene vertebrates, especially mammals, along the Madre de Dios/Acre River (Fig. 1A; Frailey, 1986). One of the most notable discoveries of these campaigns was *Amahuacatherium peruvium*, a gomphotheriid proboscidean of disputed affinities and age, which was unearthed from an outcrop of the Madre de Dios River, nearby the confluence with the Los Amigos River (=Cerro Colorado section; Campbell et al., 2000, 2001, 2010; Alberdi et al., 2004; Ferretti, 2008; Mothé & Avilla, 2015). Located in a high cliff with extensive landslides, the concerned section ranges from the late Miocene up to the late Pleistocene, as constrained by magnetostratigraphy (Campbell et al., 2010), radioisotopy, and geomorphology (Olivier et al., 2009). A Pleistocene thorny bamboo, referred to as *Guadua* sp., was recognized in blue clays located 6 m below the top of the same cliff (Olivier et al., 2009).

The discovery of the Santa Rosa locality, in eastern Peru (Fig. 1A) represented a real milestone, as it included the first indisputable species-rich Paleogene vertebrate assemblage from Proto-Amazonia. It led to the publication of a monograph (Campbell, 2004), mainly focusing on mammals, including rodents (Frailey & Campbell, 2004), marsupials (Goin & Candela, 2004), a possible gondwanathere (Goin et al., 2004), bats (Czaplewski & Campbell, 2004), and notoungulates (Shockey et al., 2004). It also yielded cingulate xenarthrans, described by Ciancio et al. (2013), and the earliest and basalmost South American primate described thus far (Bond et al., 2015). In the absence of any other temporal constraint except mammalian biochronology (which has been difficult, since most Santarosan taxa are new to

science and endemic), the age of this locality remains unclear: it may be either "?late Eocene" (e.g., Bond et al., 2015) or, more probably, early Oligocene (Shockey et al., 2004; Croft et al., 2009: 197; Antoine et al., 2012; Kay, 2015).

In the last decade, field efforts were also undertaken in the Fitzcarrald Arch (Fig. 1A), the topographic high bordering upper Amazonian sub-basins (see Espurt et al., 2010). These field campaigns enabled the discovery of a rich and diversified vertebrate fauna, assigned to the late middle Miocene Laventan South American Land Mammal Age (SALMA), and dominated by mammals, fish, and crocodylomorphs ('Fitzcarrald Local Fauna'; Salas-Gismondi et al., 2006, 2007; Antoine et al., 2007; Negri et al., 2010; Goillot et al., 2011; Pujos et al., 2013; Tejada-Lara et al., 2015). Simultaneously, the same multidisciplinary team performed reconnaissance surveys along the upper Madre de Dios River (Fig. 1A), leading to the recognition of an early Miocene mammalian faunule, with the earliest crown platyrrhine known so far (MD-61, "Pinturan" age; Marivaux et al., 2012), and an early middle Miocene mammal assemblage ("Colloncuran" SALMA; Antoine et al., 2013). Based on microfossils (foraminiferans), macrofossils (oysters and selachians), geochemical, and sedimentological evidence, that area also testified to the occurrence of a (late) Paleocene marine incursion in the Southern Peruvian Foreland Basin (SPFB; Louterbach et al., 2014). A large early Eocene xenungulate mammal, of both Patagonian and eastern Brazilian affinities, was recently recovered in northwestern coastal Peru, further indicating that South American subaerial areas formed a single biogeographic realm in early Paleogene times (Máncora locality, Fig. 1A; Antoine et al., 2015).

In Brazil, pre-Pleistocene fossils were unearthed late in the 19th century, with the giant Miocene caiman *Purussaurus*, from the Alto Purus River banks (Fig. 1A; Barbosa-Rodrigues, 1892). Since then, the Amazonian fossil record around the Brazilian-Peruvian border has been widely explored by intense fieldwork along the Madre de Dios River, the Purus River, and in

the Alto Juruá (Fig. 1A). Published works focus mainly on vertebrates (Paula Couto, 1956; Simpson & Paula Couto, 1981; Frailey, 1986; Kay & Frailey, 1993; Cozzuol, 2006; Kay & Cozzuol, 2006; Negri et al., 2010; Ribeiro et al., 2013; Kerber et al., 2015), mollusks, and ostracods (Muñoz-Torres et al., 2006; Wesselingh et al., 2006, Wesselingh & Ramos, 2010; Gross et al., 2013).

In Colombia, fossils found at the Cerrejón Coal Mine (Cerrejón Fm., Guajira; Fig. 1A) include fossil leaves, seeds, fruits and a diverse record of pollen and spores (Jaramillo et al., 2007; Doria et al., 2008; Herrera et al., 2008; Wing et al., 2009). This locality also yielded the most complete and diverse middle–late Paleocene (~59 Ma) tropical South American fauna (e.g., Cadena, 2014). This assemblage notably encompasses a giant snake (Head et al., 2009), crocodiles (Hastings et al., 2010, 2011), and turtles (Cadena et al., 2010). Regarding vertebrates, chelonian remains are by far the most abundant for the Paleogene interval in Colombia (e.g., upper Paleocene Bogotá Fm.; lower Oligocene Mugrosa Fm.; upper Oligocene Tuné Fm.; Cadena, 2014). The Neogene period is mostly documented in two distinct areas, near the Colombian-Venezuelan border (La Guajira Peninsula; Fig. 1A; fluvio-lacustrine to marine environments; lower-middle Miocene Uitma-Jimol-Castilletes Formations; e.g., Moreno et al., 2015) and in the Huila Department (La Venta area; fluviolacustrine environments; middle Miocene Villavieja and La Victoria Formations; e.g., Stirton, 1953; Kay & Madden, 1997). The middle Miocene La Venta fauna is one of the few diverse Cenozoic vertebrate faunas in tropical South America (Fig. 1A; e.g., Hirschfeld & Marshall, 1976; MacFadden, 1990, 2006; Lundberg, 1997; Madden et al., 1997). The fossil mammals consist of marsupials, xenarthrans, rodents, astrapotheres, litopterns, toxodonts, typotheres, primates, sirenians, and bats (Kay & Madden, 1997; Czaplewski et al., 2003). Mollusk, arthropod, and vertebrate faunas from La Guajira Peninsula and the Socorro-Urumaco Formations in Venezuela (Fig. 1A) further indicate the presence of biotic

connections between the paleo-Amazonas-Orinoco system and coastal areas of Colombia-Venezuela during Neogene times (Sánchez-Villagra et al., 2000, 2004; Sánchez-Villagra & Scheyer, 2010; Rincón et al., 2014; Hendy et al., 2015, Jaramillo et al., 2015; Moreno et al., 2015; Salas-Gismondi et al., 2015; Vallejo-Pareja et al., 2015).

In contrast with the Andean highlands (for a review, see Flynn et al., 2012), little work has been done on the Cenozoic fossil record of Amazonian lowlands from Bolivia (e.g., Hulka et al., 2006; Uba et al., 2009; Tineo et al., 2015) and Ecuador (e.g., Tschopp, 1953).

Most of these localities represent a suite of snapshots in the history of Proto-Amazonia and/or glimpses into the evolutionary history of a given taxonomic group, which are not easily temporally correlated within a single time frame, although synthetic works have paved the way: Hoorn (1993) and Jaramillo et al. (2011) for Neogene and Cenozoic palynostratigraphy, respectively; Wesselingh et al. (2006) for Miocene mollusks; Sheppard and Bate (1980), Muñoz-Torres et al. (1998), Ramos (2006), Wesselingh & Ramos (2010), or Gross et al. (2013; 2014) for ostracods and/or foraminifers; Lovejoy et al. (1998, 2006), Monsch (1998), Brito & Deynat (2004), Brito et al. (2007), and Lundberg et al. (2010) for fish evolution and distribution; Negri et al. (2010) for mammals and birds; Hovikoski et al. (2010), Lundberg et al. (2010), Boonstra et al. (2015) for sedimentological and paleontological arguments of Miocene marine incursions.

The region of Contamana, in Loreto, Peruvian Amazonia (Fig. 1A-B), is a notable exception at the Amazonian basin scale. Today, Contamana is located in the North Amazonian foreland basin, NW of the Fitzcarrald Arch, and near the Ucayali River (Fig. 1). Due to Andean tectonics, this area is folded with NW-SE structures (Fig. 2), which provides access to a thick stratigraphic section documenting an extremely long and continuous sedimentary record (Jurassic-Holocene), unparalleled at the Amazonia scale. The section was thoroughly described and measured for "petroleum prospects" by the *Comisión Geológica de*

la Montaña during the 1940s in two distinct zones, i.e. along the Cushabatay River and the Cachiyacu River (the latter hereunder denoted as Quebrada Cachiyacu; Kummel, 1948). Yet, the corresponding fossil content, suggested to be rich and quite diversified (Kummel, 1948), was never collected nor properly described. For instance, the geological map of the Contamana area (Lipa et al., 1997) provides a paleontological appendix restricted to a single charophyte assemblage, originating from an early Paleogene interval (Fig. 1A; see section 3.1.1; Romero-Pittman in Lipa et al., 1997).

1.2. New fieldwork

Since 2008, seven annual field expeditions by a multidisciplinary international team have taken place in the Contamana area, with the aim of comprehensively surveying the Cenozoic deposits along the Quebrada Cachiyacu. This long-term survey resulted in the discovery of scattered outcrops on mud trails and on the new road to Quebrada Agua Caliente (Figs. 1A-2). In total, at least 34 fossil-yielding localities have been identified, which have yielded vertebrate remains (fish, amphibians, sauropsids, and mammals) as well as mollusks, arthropods (ostracods and crustaceans), plant fossils (palynomorphs, charophytes, seeds, fruits, and silicified wood), microfossils (foraminiferans, poriferans, and algae), and dinoflagellates, as listed in the Supplementary Data. In a single continuous section on the SW flank of the Maquía Anticline, we recognize 20 successive fossil-bearing levels, ranging from the middle Eocene up to the late Miocene-?Pliocene, in the SW flank of the Maquia Anticline (Fig. S1). The main characteristics of all concerned localities are detailed in the Table 1.

Two recent studies by our team have focused on a fossil-rich level from the Quebrada Cachiyacu (namely CTA-27; Figs. 2-3), that is late middle Eocene in age, around the Lutetian-Bartonian transition. To date, this locality has yielded both the earliest South American hystricognathous rodents (stem Caviomorpha; Antoine et al., 2012) and freshwater

stingrays (Potamotrygonidae; Adnet et al., 2014). Yet, the thanatocoenosis of all other levels from the same Contamana area remains to be described and characterized.

Based on this unrivalled paleontological corpus, the current work documents ~60 million years of life history in the Neotropical lowlands (early Paleocene to ?Pliocene), with a focus on the biotas and their physical environment, spanning the final stages of Proto-Amazonia and the onset of modern Amazonia.

2. Material and methods

2.1. Material

All fossils described in the present work were found in-situ by our team in the Contamana area, while prospecting or excavating during the 2008–2014 field campaigns (see Supplementary Data). Small remains (microvertebrates, arthropods, mollusks, and charophytes) were collected by screening-washing of rock samples ranging from 200g (preliminary tests) up to ca. 850kg (e.g., CTA-27, CTA-32, CTA-61, CTA-44, and CTA-43), with a 0.7mm and/or 1mm and/or 2mm mesh. No acid etching has been done, in order to preserve delicate calcified shells (foraminiferans, mollusks, ostracods, and crabs). Each and every specimen recognized *a priori* as belonging to a fossil organism was collected in the field, then adequately preserved, and subsequently studied by the colleague with the most extensive experience on the taxonomic group concerned. Taxa already described from the Cachiyacu section (rodents [Antoine et al. 2012] and freshwater stingrays from CTA-27 [Adnet et al. 2014]) will not be described herein, but the corresponding results will be taken into account for the discussion. Specimens were tentatively identified at species level

whenever possible. Nonetheless, many of them have a formal taxonomic assignment above the species or the genus level (see Supplementary Data). The fossils that were left in open nomenclature are either (*i*) lacking diagnostic features (often due to their fragmentary state) or (*ii*) likely to document new taxa to be described in the near future in dedicated papers, which is far beyond the scope of the present work. The specimens are stored in the *Museo de Historia Natural, Universidad Nacional Mayor de San Marcos*, Lima, Perú (MUSM).

Localities (termed CTA-XX and ranked by order of recognition in the field) were named separately when consisting of distinct outcrops. In very few cases, lateral equivalences were subsequently and unambiguously recognized based on geometrical and/or lithostratigraphical and/or paleontological correspondences between close exposures (e.g., CTA-41 and CTA-53 or CTA-44 and CTA-58; Fig. 3). In few other cases, distinct stratigraphic levels were distinguished within a single thick exposure, where distinct depositional environments were suspected to occur (i.e., marine-influenced vs. fluvial settings in CTA-44). Fossil-yielding levels usually are 10cm up to 50cm-thick. None of them is more than 1m-thick. The hypothesized sedimentation rates as calculated by Roddaz et al. (2010: table 5.2) for the Northern Peruvian foreland basin are around 1mm/year. As a consequence, time-averaging within a given locality is considered negligible, especially given that the complete fossil-yielding series is ca. 2,800m-thick, with a continuous record exceeding 1,300m for the middle Eocene–?Pliocene interval (Fig. 3).

Upper case letters are used for upper dentition (I, for incisor; C, for canine; P, for premolar; M, for molar; D, for decidual teeth) and lower case letters for lower dentition (i, for incisor; c, for canine; p, for premolar; m, for molar; d, for decidual teeth). All measurements are given in millimeters, except when mentioned.

Institutional Abbreviation: MUSM, *Museo de Historia Natural de la Universidad Nacional Mayor San Marcos*, Lima, Perú.

Other abbreviations: FAD, First Appearance Datum; FLO, First Local Occurrence; Fm., Formation; GABI, Great American Biotic Interchange; LAD, Last Appearance Datum; LLO, Last Local Occurrence; NPFB, Northern Peruvian foreland basin; PMWS, Pebas Mega-Wetland System; SALMA, South American Land Mammal Age; SPFB, Southern Peruvian foreland basin.

2.2. Methods

2.2.1. Lithostratigraphy

The nomenclature of Cenozoic formations from the Contamana area mostly follows that proposed in the seminal monograph by Kummel (1948) and subsequent works (e.g., Christophoul et al., 2002; Hermoza et al., 2005; Roddaz et al., 2010 and references therein; Louterbach et al., 2014).

2.2.2. Chronostratigraphy

The chronostratigraphy for the Cenozoic deposits of Contamana (Quebrada Agua Caliente and Quebrada Cachiyacu sections) was achieved by combining biochronological proxies (nanofossils: dinoflagellates; microfossils: spores and pollen, charophytes, foraminiferans, and ostracods; macrofossils: mollusks and vertebrates) and radioisotopic data (Ar/Ar on feldspars; U/Pb on zircon grains).

Biochronological proxies: All fossil specimens we have collected in-situ during 2008–2014 were regarded *a priori* as potentially useful in a biostratigraphical perspective. The concerned specimens were then investigated independently by specialists of the corresponding taxonomic groups. Biochronological inferences were provided agnostically, discussed in detail, and then synthesized to be presented here. In most cases, geo- and biochronological results derived from the different taxonomic groups were consistent. Yet, as exemplified by the early Oligocene Tinguiririca Fauna (Fig. 1A), first described by Flynn et al. (2003) as bridging a gap between early late Eocene (Mustersan SALMA) and late Oligocene (Deseadan SALMA) mammalian faunas, some of the richest faunal assemblages from Contamana may document the co-occurrence of several taxa previously thought not to be coeval at the South American scale. This is particularly true for charophytes, mollusks, decapods, or vertebrates.

Palynostratigraphy has been used as the main biostratigraphic tool by numerous oil companies and researchers in the region over the last 50 years, with excellent results (Germeraad et al., 1968; Regali et al., 1974; Bayona et al., 2008; Jaramillo et al., 2009). The palynological zones used in the region (Germeraad et al., 1968; Lorente, 1986; Muller et al., 1987; Hoorn, 1993; Jaramillo et al., 2011) have been calibrated with planktonic foraminifera and carbon isotope stratigraphy (Germeraad et al., 1968; Muller et al., 1987; Carvajal-Ortiz et al., 2009; Jaramillo et al., 2011).

Radioisotopic methods: The tuff CTA-29 (Figs. 2-3) was dated by $^{40}Ar/^{39}Ar$ laser step heating on feldspar grains, following a protocol detailed in Antoine et al. (2012). The tuff CTA-08SA (Figs. 2-3) was previously correlated with CTA-29 (Antoine et al., 2012). However, fieldwork performed in 2012-2014 allowed for the discovery of new outcrops, including both fossil-yielding localities (e.g., CTA-66, CTA-73) and ash-levels (e.g., CTA-

67). Together with new dating proxies (U/Pb dating of zircon grains from CTA-08SA by one of us [FC]), this additional corpus has enabled us to provide a far more complete scenario for correlating both flanks of the Maquía Anticline (Supplementary Data), and to build up a consistent synthetic section (Fig. 3).

In particular, the age of CTA-29 (NE flank; Fig. 2) has not changed (43.44±2.5Ma, on feldspar grains); this ash is now tentatively correlated with CTA-67 (SW flank; Fig. 2), based on all available dating proxies. CTA-08SA is located much higher in the stratigraphic section, which is consistent with both its radioisotopic age (26.56±0.07 Ma; U/Pb on zircon grains) and the fossil content of surrounding levels (i.e., CTA-61 and CTA-62, discovered in 2012; Fig. 2).

The CTA-08SA tuff contains zircons that are generally subrounded and with a variety of appearances, suggesting that they are mostly detrital. A selection for analysis was made using zircon crystals that preserve euhedral crystal faces with no evidence of sedimentary damage likely to further coincide with a long gap before deposition. The crystals were treated with chemical abrasion (Mattinson, 2005) to remove effects of secondary Pb loss, and were then analyzed by ID-TIMS as described for this lab by Corfu (2004). Decay constants are from Jaffey et al. (1971). The analyses, reported in Table S1, indicate that at least five of the grains are detrital: one of them is Precambrian (ca. 1,100 Ma), one Permian (264 Ma) and the other three latest Eocene to Oligocene in age. The youngest crystal gives an age of 26.56 ± 0.07 Ma (Fig. S2; Table S1), which is likely to be close to the time of eruption/deposition.

3. Results

3.1. Lithostratigraphic units and fossil assemblages

In the following section, formations will be described in stratigraphic order, with a special emphasis on their context, exposures, thickness, paleontological content, inferred time range, and depositional environment(s).

From the bottom up to the top of the Cenozoic series, we have recognized the base of the Huchpayacu Fm. (early Paleocene), the Pozo Fm. (middle + ?late Eocene), and complete sections for the Chambira Fm. (late Oligocene–late early Miocene), the Pebas Fm. (late early to early late Miocene), and Ipururo Fm. (late Miocene–?Pliocene). The Ucayali Fm. (Pleistocene) was not investigated from a paleobiological perspective during our fieldwork. Due to intense surface weathering and vegetation cover, the Casa Blanca Fm. (white sandstones, ?Paleocene–Eocene in age; cropping out in the Cushabatay section; Kummel, 1948) could not be identified during our fieldwork.

3.1.1. Huchpayacu Formation (Paleocene)

Description: In the Contamana area, the lowermost part of the Cenozoic section is only observed in the Agua Caliente section, where gray charophyte-rich marls and limestones crop out in a single 10m-thick exposure (CTA-54; Fig. 1A; Table 1). It seemingly overlays conformably the Campanian-Maastrichtian marine black shales referred to the Cachiyacu Fm. in the same section. This unit was initially described as representing the lowermost strata of the Yahuarango Fm. by Kummel (1948: 1259; "marl, gray, filled with charophytes") and Romero-Pittman in Lipa et al. (1997). Yet, such a succession recalls the situation depicted by Kummel (1948: 1257) in the Quebrada Cushabatay section ~100 km to the NW and in the Río Cashiboya by Romero Pittman in Lipa et al. (1997), ~25 km to the SE (Fig. 1A). Accordingly, we assign this charophyte-rich level to the Huchpayacu Fm. instead of the Yahuarango Fm. We could observe neither the supposedly overlying deposits of the Casa Blanca Fm. (white massive sandstones, 60 m-thick in the Cushabatay area; Kummel, 1948) nor the hypothetic

Yahuarango Fm. sensu stricto (see Roddaz et al., 2010 for further discussion), that were irremediably weathered and completely covered by vegetation. Nevertheless, given the dipping observed for Cenozoic deposits in the concerned sections, the basal Huchpayacu marls and limestones can be estimated as being located about 1,500 m below the base of the lowermost levels observed in the Maquía Anticline, and here referred to the Lower Pozo Fm. (Figs. 2-3), i.e. to the Upper Member of the Yahuarango Fm. sensu Kummel (1948) and Antoine et al. (2012). This is in good agreement with the thickness of the corresponding interval, as proposed by Kummel (1948) based on direct observation in the "*Cerros de Contamana*" (8 km further to the NE from the syncline core denoted by "B" in Fig. 2) – a remote zone we did not investigate.

Paleontological content (Fig. 4). Screening-washing of ~4.5 kg of sediment at CTA-54 (Fig. 1A) has allowed for the recovery of thousands of charophyte gyrogonites (Fig. 4), associated with unidentified bone fragments (Vertebrata indet.) and inner casts of gastropods, but no pollen. The corresponding charophyte assemblage includes fourteen taxa, referred to as *Chara* "*Grambastichara*" *subcylindrica* (Fig. 4A), *Sphaerochara inconspicua* (Fig. 4B), *S. huaroensis* (Fig. 4C-E), *Nitellopsis supraplana sulcata* (Fig. 4F-H), *N.* (*Tectochara*) *merianii* (Fig. 4I-J), *Peckisphaera* cf. *portezuelensis* / *Peckichara* sp. (Fig. 4K-M), *Peckichara* cf. *varians* (Fig. 4N), *Peckichara* sp., *Pseudolatochara* sp., *Chara*? sp., *Lamprothamnium* sp., *Brevichara* sp., *Platychara* cf. *perlata*, and Characeae indet. This assemblage encompasses morphospecies of South American, Gondwanan, or cosmopolitan affinities (Table 2).

Age: Based on the charophyte assemblage documented in CTA-54, the base of the Huchpayacu Fm. can be somewhat constrained in terms of biostratigraphic age (Table 2). Aside from panchronic taxa, such as *Nitellopsis* (*Tectochara*) *merianii*, *Chara*? sp., or *Brevichara* sp., most taxa converge toward a Paleocene age for CTA-54 (*Chara* "*Grambastichara*" *subcylindrica*, *Sphaerochara inconspicua*, *Nitellopsis supraplana sulcata*,

Peckichara sp., *Peckichara* cf. *varians*, *Pseudolatochara* sp., *Lamprothamnium* sp.; Mourier et al., 1988; Musacchio, 2006; Mebrouk et al., 2009; Vialle et al., 2013). *Sphaerochara huaroensis* and *Platychara* cf. *perlata* have early Paleocene LADs (Jaillard et al., 1993, 1994; Louterbach et al., 2014). Accordingly, the "*Sphaerochara* Zone" as defined in the Peruvian Andes is early Paleocene in age (Jaillard et al., 1993, 1994), which further supports a Danian age for CTA-54. The co-occurrence of *Peckisphaera* cf. *portezueloensis*, of latest Cretaceous affinities (Musacchio, 1973; Chassagne-Manoukian et al., 2013), with several *Sphaerochara* species (early Paleocene), is not in conflict with this hypothesis.

The charophyte assemblage as described by Romero-Pittman in Lipa et al. (1997) along the Río Cashiboya (Fig. 1B) and including *Sphaerochara brevesterensis*, *Tectochara supraplana supraplana* (=*Nitellopsis supraplana supraplana*), *Tectochara ucayalensis ucayalensis*, and *T. u. gradata*, might document the same "*Sphaerochara* Zone" (Jaillard et al., 1994). Accordingly, we assume an early Paleocene age for this level as well.

There are no charophyte species in common between CTA-54 (Huchpayacu Fm.) and any locality assigned to the Pozo Fm. (Supplementary Data), which further supports the presence of a long stratigraphic gap between both rock units.

Depositional environment: The high abundance of charophyte oogonia and the occurrence of grayish limestones and violine marls testify to poorly drained lacustrine and/or fluvial environments, in good agreement with the conclusions of Romero-Pittman in Lipa et al. (1997), at least for the documented outcroup/interval (base of the Huchpayacu Fm. in CTA-54).

Correlation: From North to South, comparable formations have been recognized in Northern Peru (Rentema Fm., around Bagua: Mourier et al., 1988; Naeser et al., 1991; in the Huallaga Basin: Hermoza et al., 2005), in Peruvian Andes (around Cuzco: Jaillard et al.,

1994), in Southern Peru (Gil et al., 2001), and in Bolivia (Santa Lucía Fm.; e.g., Gayet et al., 2003).

3.1.2 Pozo Formation, Lower Member; 'Pozo Sands' (middle and ?late Eocene interval)

Description (Fig. 5): As noticed above, only the lower member of the Pozo Fm. crops out in the Quebrada Cachiyacu profile at Maquía (300 m-thick in the SW flank of the anticline and 500 m-thick in the NE flank; Fig. 2B; Fig. S1). However, this interval is widely exposed, as these deposits form the core of the Maquía Anticline (Fig. 2). They consist essentially of red mudstones and variegated paleosols (blue, yellow, red, and purple) with anhydrite veins locally, alternating with scattered infra-metric channelized sandstone lenses (Fig. 5A-B), most of which have yielded a diversified fossil content (Fig. 6; Supplementary Data). In exposures such as CTA-51, CTA-27 (Fig. 5B), CTA-29 or CTA-66 (Fig. 5D), these sandstones are massive, gray to yellowish, and unconsolidated. They include millimetric calcareous nodules of diagenetic origin (Fig. 5D), locally encrusting fossil elements (charophyte oogonia, crab claws, fish scales and vertebrate teeth and bones). In some places (e.g., CTA-41), millimetric red clay pebbles occur within microconglomerates.

The concerned unit includes a 30cm-thick red-brown tuffaceous silty sand exposed in the NE flank of the Maquía Anticline (CTA-29; Figs. 2-3, 5C; Fig. S1). It was dated by Ar/Ar on feldspar grains (43.44±2.5 Ma; see Antoine et al., 2012) and, based on lithostratigraphy, it is considered to be laterally equivalent to a tuffaceous level cropping out in the SW flank of the Maquía Anticline (CTA-67; Figs. 2-3; Fig. S1). No fossil-yielding outcrop referable to the Pozo Fm. was recognized in the Agua Caliente section.

Paleontological content (Fig. 6): In the Quebrada Cachiyacu section, 11 fossiliferous outcrops are referred to the Lower Pozo Fm. They document unambiguously nine successive levels (from the base upward, CTA-48, CTA-47+60, CTA-51, CTA-27, CTA-73, CTA-50,

CTA-41+53, CTA-29, and CTA-66; Figs. 2-3; Fig. S1). Most (if not all) fossiliferous levels yield numerous ostracods (Cypridacea and Cytheracea; e.g., *Neocyprideis apostolescui* and *Ilyocypris* aff. *lusitanica* in CTA-27; Fig. 6G-H) and charophyte gyrogonites (13 taxa, widely dominated by *Raskyella pecki meridionale*; Fig. 6B-D; Table 2), which strongly contrasts with the overlying deposits from the Chambira, Pebas, and Ipururo Fms. (not a single ostracod recovered, only one charophyte-yielding locality; Table 2). The most diversified assemblage is CTA-27 (Antoine et al., 2012; Adnet et al., 2014). It encompasses plant remains (silicified wood chunks and seeds; charcoal; charophytes; Table 2) and palynomorphs (first listed in Antoine et al., 2012). The pollen assemblage from CTA-27 is diverse and well preserved (Table S3). The concerned palynoflora is strictly continental and it indicates a tropical rainforest habitat, with no evidence of savanna vegetation. Palynoflora is composed by a rich diversity of rainforest taxa including *Spirosyncolpites spiralis* (Fabaceae), *Striatopollis catatumbus* (Fabaceae), *Tetracolporopollenites maculosus* (Sapotaceae), *Perisyncolporites pokornyi* (Malphigiaceae), among many others. The faunal community from CTA-27 includes mollusks (pachychilid gastropods and bivalves; Fig. 6J), crustaceans (ostracods and trichodactylid crabs; Fig. 6I; Yeo et al., 2014), and 49 vertebrate taxa. The concerned vertebrate fauna (Fig. 6L-AF) includes freshwater stingrays (*Potamotrygon ucayalensis* Adnet et al., 2014), characiform actinopterygians (Fig. 6L-N), anurans (pipid and 'leptodactyloid'), snakes (anilioid and booid), a lizard (platynotan?), chelonians, crocodylomorphs (*Sebecus*; gavialoid and caimanines; Fig. 6P-Q), a wide array of metatherians (didelphimorphs, sparassodont, bonapartherioid and prepidolopid polydolopimorphians, as well as palaeothentoid paucituberculatans; Fig. 6R-Z), the astegotheriine dasypodid *Stegosimpsonia* cf. *chubutana*, five caviomorph rodents, notoungulates, an astrapothere, a litoptern, and a pyrothere (Fig. AC-AE; for further details, see Antoine et al., 2012), but also probable microchiroptere bats, for a total amount of 26

mammalian taxa (Supplementary Data). One tooth of a (possible) gondwanathere mentioned in CTA-27 by Antoine et al. (2012) would more likely be an upper premolar referable to a polydolopimorphian marsupial. However, two other fragmentary teeth are still potentially referable to gondwanatheres.

Other localities, either situated below (e.g., CTA-47 [Fig. 5A] or CTA-51) or above CTA-27 in the section (e.g., CTA-29 or CTA-66; Figs. 3, 5C-D) do yield highly analog assemblages (especially regarding charophytes [Table 2], ostracods, potamotrygonid selachians, osteichthyans, crocodiles, rodents, and metatherians; Figs. O, AA-AB), although less species-rich (Supplementary Data). Only CTA-29 provides further information on xenarthrans, with an unidentified tolypeutine dasypodid and a cingulate (Fig. 6AB) showing close affinities with *Eocoleophorus* from the late Oligocene of Taubaté, Brazil and Salla, Bolivia; Salas-Gismondi et al., 2011) and *Yuruatherium* from the late Eocene-early Oligocene of Argentina and Peru (Ciancio et al., 2013).

Overall, the fossil assemblages recovered throughout the Lower Member of the Pozo Fm. in Contamana seem to document a single phase of Proto-Amazonian ecosystems, under stable conditions, by late middle Eocene times (Barrancan age; Antoine et al., 2012; Woodburne et al., 2014).

Age: As the upper Member of the Pozo Fm. seems not to crop out in the studied area, no age range can be ascertained for the complete formation. However, based on both mammalian biostratigraphy and palynostratigraphy (Antoine et al., 2012), and radioisotopy (Ar/Ar on feldspars in CTA-29; Fig. 5C; Antoine et al., 2012), the exposed unit is unambiguously assigned to the late middle Eocene (from CTA-48 up to CTA-29 [NE flank] and CTA-66 [SW flank]; Fig. 3; Fig. S1). The CTA-27 locality is estimated at ~41 Ma on the same ground (Antoine et al., 2012), coinciding with the early Bartonian stage (Vandenberghe et al., 2012) and the Barrancan age (Casamayoran SALMA; Woodburne et al., 2014). Depending on the

species concerned, charophytes from the Lower Member of the Pozo Fm. (Table 2) span the Santonian-early Oligocene interval (e.g., *Lychnothamnus* (*Pseudoharrisichara*) *tenuis* and *Lychnothamnus major*, respectively; Musacchio, 2010; Sanjuan & Martín-Closas, 2012), with a strong Eocene signature (*Raskyella pecki meridionale*, *Nodosochara jorbae*, and *Stephanochara acris*; Martín-Closas & Guerrero, 2005; Adaci et al., 2007; San Juan & Martín-Closas, 2014). The ostracods further support an Eocene age for the fossiliferous part of the Pozo Fm. on the Contamana area, based on the co-occurrence of *Neocyprideis apostolescui* (middle-late Eocene; Mebrouk et al., 2011) and *Ilyocypris* aff. *lusitanica* (earliest Eocene affinities; Colin & Antunes, 2003).

Given the preserved thickness of the Lower Pozo Fm. above CTA-29 in the NE flank of the Maquía Anticline (~300 m), its top is likely to record the late Eocene interval.

Depositional environment: The exposed part of the Pozo Fm. (300–550 m-thick) consists only of thin lenses of reddish silt and yellowish sandstone, of fluvial origin, alternating with thick intervals of variegated paleosols and distal floodplain deposits (Fig. 5A). Some levels scattered throughout the exposed units show thick interwoven anhydrite veins, pointing to the probable occurrence of contrasted seasons. The paleontological content (charophytes, pollen, and spores; decapods, mollusks, and ostracods; fish, crocodylomorphs, and mammals; Fig. 6) is mostly of continental affinities, either aquatic or terrestrial/arboreal (Antoine et al., 2012; Adnet et al., 2014). In the entire studied area, the only evidence for a marine influence during the concerned interval is the co-occurrence of dinoflagellates *Cleistosphaeridium*, *Leiosphaeridia*, and *Spiniferites* in the lowermost observable level (CTA-47; Table S3). This marine influence may coincide with what is reported on coeval deposits from the Huallaga area (marine and/or tide-influenced Pozo Fm.; Hermoza et al., 2005). Above in the Pozo Fm., a single ostracod recognized in CTA-27 (*Neocyprideis apostolescui*; Fig. 6G) may indicate euryhaline-mesohaline conditions, but this taxon is known to be tolerant to salinity changes,

and further associated with a fauna and flora of strict freshwater affinities, without any marine influence (Antoine et al., 2012; Adnet et al., 2014).

In the Contamana area, the Upper Pozo Fm. was most probably eroded, and then unconformably overlain by deposits of the Chambira Fm. after differential vertical movements at local and/or regional scale. This hypothesis is supported by a strong discrepancy in the preserved thickness of the Pozo Fm. above the marker ash (Fig. S1), between the SW flank of the Maquía Anticline (Pozo/Chambira transition ~50 m above the ash at CTA-67) and its NE flank (Pozo/Chambira transition ~300 m above the ash at CTA-29).

Correlation: These levels can be correlated with those of the Cruzeiro Formation in the upper Yuruá ("red beds" at the Peru/Brazil border; Oppenheim, 1937). The concerned time range also coincides with the interval documented by the Pozo Fm. of the NPFB, the age of which was constrained by low-temperature thermochronology (Hermoza et al., 2005; Roddaz et al. 2010). Although documenting somewhat distinct depositional environments (freshwater-dominated in the Ucayali basin; marine/tidal-dominated in the Huallaga basin), both units are laterally equivalent. 'Pozo Sands' in the Huallaga and Marañon basins (NPFB) are considered laterally equivalent to the Upper Tiyuyacu Fm. in the Oriente basin of Ecuador, which is capping a important erosional unconformity with strong geodynamic significance (Christophoul et al., 2002). This interval is not unambiguously documented in the SPFB (see Louterbach et al., 2014 for a review).

3.1.3. Chambira Formation (Oligocene–?early Miocene)

Description (Fig. 7): In the Contamana area, coarser deposits of the Chambira Fm. overlay unconformably the variegated paleosols and silts of the Lower Pozo Fm.

On both flanks of the Maquía Anticline, the Chambira Fm. mainly consists of thick compounds of red paleosols, with intercalated conglomerates and sandbars (with trough and planar cross-stratifications; CTA-74) at the base. The base of the Chambira Fm. is defined by the lowermost channelized conglomerates showing both sharp quartz pebbles and multicolor volcanic/metamorphic clasts and a sandy matrix (CTA-62; Figs. 2-3; Fig. S1). Another conglomerate with similar characteristics (CTA-61; Fig. 7C) occurs 15 m above the latter level in the SW flank, further attesting to a drastic change in the regional sedimentary dynamics. On the NE flank of the Maquía Anticline, a 50 cm-thick and 10 m-wide fluvio-lacustrine channel (CTA-32; Figs. 2-3) is located ~30m above the basal conglomerate (Fig. S1). This lens consists of a 15 cm-thick conglomerate with centimetric pebbles of fluvial origin, topped by bluish lacustrine clays, which have yielded an abundant and species-rich vertebrate fauna (CTA-32; Fig. 7A-B; see Supplementary Data).

The middle and upper parts of the Chambira Fm. provided no fossil record except for a tree stump of an unidentified dicot (CTA-78; Figs. 2, 7D). They are essentially documented by red paleosols intersected locally by anhydrite veins, with rare intercalated sandbars. A remote and species-poor vertebrate locality, situated on the road to Agua Caliente (CTA-72; Fig. 1B; Supplementary Data), is correlated to an unidentified term of the Chambira Fm., based on both its extrapolated stratigraphical position and compatible facies (red paleosol with anhydrite veins).

The total thickness of the Chambira Fm. is 180 m in the SW flank of the Maquía Anticline (Figs. 3, S1). In the NE flank, the transition seems to be gradational with the Pebas Fm. and we have not recognized any unquestionable level referable to the latter in the Cachiyacu syncline. It is impossible to estimate properly any thickness for the Chambira Fm. in the Agua Caliente section.

Paleontological content (Fig. 8): The Chambira Fm. in the Contamana region encompasses only five fossil-yielding localities, widely dominated by vertebrates, in three distinct areas: three successive levels are recorded in the SW flank of the Maquía Anticline (from the base to the top, CTA-62, CTA-61, and CTA-74; Fig. 2); a single locality, interpreted as documenting both a sub-coeval interval and distinct environmental conditions, was uncovered in the NE flank of the Maquía Anticline (CTA-32; Figs. 2, 7A-B, S1); the last one, CTA-72, was found in 2014 on the road to Agua Caliente. Its fossil content is of poor taxonomic and stratigraphical interest (Figs. 1-2; Supplementary Data). There is no palynological record for the entire Chambira Fm. in the Contamana area. Two fossiliferous localities are especially species-rich (CTA-32 and CTA-61).

CTA-32 yielded fossil wood, crabs, and 43 vertebrate species (Fig. 8A-F, N-R; Supplementary Data). This assemblage includes potamotrygonid freshwater stingrays, a wide array of osteichthyans (serrasalmine, anostomid, cynodontid, erythrinid, and characid characiforms (Fig. 8A); pimelodid and loricariid siluriforms; a perciform), anurans (at least one non-pipid), snakes (two booids and two non-booids, including a possible colubroid), chelonians, four crocodylomorphs (a sebecid, two caimanines, and a gavialoid), a bird, plus 24 mammalian taxa. Five metatherians are recognized: a stem metatherian (?herpetotheriid), a ?palaeothentid and two abderitid paucituberculatans (*Abderites* sp. and cf. *Abderites*; Fig. 8D-E), and a microbiotheriid. Placentals are represented by scutes referable to cingulate xenarthrans (cf. *Neoglyptatelus*, of uncertain affinities; a pampatheriid (Fig. 8F), close to *Yuruatherium* from Santa Rosa, Peru as described by Ciancio et al. (2013); a tolypeutine dasypodid), tooth fragments of native ungulates (hypsodont notoungulate, ?litoptern, and astrapotheriid astrapothere), teeth of six distinct rodents (two caviomorphs of uncertain affinities, a small erethizontid, and three octodontoids including an adelphomyine and cf. *Eosallamys* sp.; Fig. 8N), teeth of three microchiropterans (an emballonurid [Fig. 8O], an

vespertilionoid, and a ?rhinolophoid), and a pollical phalanx of an anthropoid primate (Fig. 8P-R).

The fossil assemblage of CTA-61 (Fig. 8G-M) encompasses exclusively 39 vertebrate taxa, with amphibian, snake, crocodylomorph, and chelonian components highly similar with those of CTA-32 (Supplementary Data). Yet, fish faunas widely differ between the two sites, especially as regards characiforms (a piranha-like characid, an erythrinid, a characid, and an unidentified characiform with hook-like teeth only occur in CTA-32; CTA-61 yields two unidentified characiforms with domed and tricuspid teeth, respectively), but also siluriforms (a small pimelodid and a loricariid are recognized in CTA-32; a large *Phractocephalus*-like pimelodid siluriform is recorded only in CTA-61) and perciforms (an unidentified cichlid occurs in CTA-32). Twenty-one mammalian species are recognized in that fauna. At first glance, they seem to be broadly distinct from the ones identified in CTA-32, at least at the species level (Supplementary Data). Yet, metatherians have a quite similar composition, dominated by paucituberculatans (among which cf. *Abderites*) and including the same microbiotheriid. Xenarthrans encompass a probable pampatheriid cingulate and mylodontoid sloths (Fig. 8G-H). South American native ungulates are essentially documented by notoungulates (an unidentified brachydont toxodontid and two hypselodont typotheres, i.e., an interatheriine and a hegetotheriid or archaeohyracid; Fig. 8I-K). An isolated lower premolar is referable to a litoptern and a fragmentary lower molar to an astrapotheriid. As in CTA-32, rodents are represented by chinchilloids (two species), three octodontoids (among which an adelphomyine), erethizontoids, and a cavioid (Supplementary Data). The rodent assemblage notably includes cf. *Eoincamys* sp. (Fig. 8L), *Eoespina*? sp. and *Deseadomys* sp. (Fig. 8M; not *Ethelomys* sensu Vucetich et al., 2015). Likewise in CTA-32, a primate was recognized in CTA-61. It is provisionally identified as a soriacebine homunculid.

Such discrepancies between CTA-32 and CTA-61 may coincide at first order with highly distinct conditions in terms of ecology and depositional environments (high-energy stream *vs*. steady pond in CTA-61 and CTA-32, respectively, with contrasted grain sizes engendering a systematic bias for fossil specimens), instead of documenting a significant stratigraphical gap between CTA-32 and CTA-61.

Contrary to what was observed in most fossil-yielding levels of the Pozo Fm., neither charophyte oogonia nor ostracods were recovered in the Chambira Fm. in the studied area (Table 2). Furthermore, in contrast to the fossil content of both the Pozo Fm. (below) and the Pebas Fm. (above), Chambira thanatocenoses are widely dominated by their vertebrate component in the Contamana area (no mollusk is recorded either through inner casts or shells). As regards plant fossils, only a tree stump of undetermined affinities (within dicotyledons) was recovered in the uppermost term of the Chambira Fm. (CTA-78; Fig. 7D).

Age: A 30 cm-thick tuffaceous bed (CTA-08SA) was recognized in the lowermost part of the Chambira Fm. in the SW flank of the Maquía Anticline (Figs. 2-3). We have not recovered any lateral equivalent of this bed in the NE flank. This level was dated by U/Pb on zircon grains giving an inferred age of 26.56 ±0.07 Ma, which coincides with the late Oligocene Chattian stage, and the Deseadan SALMA (Vandenberghe et al., 2012) [See Supplementary Data]. Given the local dipping, the CTA-61 locality is situated ~4m above this tuffaceous bed.

This mammalian age is mostly documented in Argentina, Bolivia (Salla), Brazil (Taubaté), Uruguay (Fray Bentos; Bond et al., 1998), and SW Peru (Moquegua; Shockey et al., 2006, 2009; Croft et al., 2009), as synthesized by Woodburne et al. (2014) and Vucetich et al. (2015). Vertebrates from the Chambira Fm. (Supplementary Data) encompass typical Deseadan taxa (abderitid marsupials, an archaeohyracid or basal hegetotheriid, and the octodontoid *Deseadomys*; Vucetich et al., 2015), as well as taxa of either earlier (the rodents

cf. *Eoincamys* sp., *Eoespina* sp., and cf. *Eosallamys* sp. [Santa Rosa; Frailey & Campbell, 2004]) or later affinities (a caenolestid, *Abderites*, the caimanine cf. *Purussaurus*, or the cingulate cf. *Neoglyptatelus*).

In the Contamana area, most available proxies (ash CTA-08SA and fossil assemblages CTA-32 and CTA-61) consistently point to a late Oligocene age for the base of the Chambira Fm (Supplementary Data). The concerned conglomerate further attests to a drastic change in the regional sedimentary dynamics, and its deposition probably coincided with the onset of a major exhumation phase in the eastern Cordillera of the Central Andes during the late Oligocene (Mora et al., 2010; Eude et al., 2015). Unfortunately, we could not find any chrono- or biostratigraphic data higher up in that formation. Yet, the level that we interpret as documenting the base of the overlying Pebas Fm. is early Miocene in age (~20-17 Ma; Colhuehuapian-Santacrucian SALMAs; see hereafter). In other words, as the Pebas Fm. conformably overlies it, the Chambira Fm. most likely spans the late Oligocene-earliest Miocene interval in the Contamana area.

Depositional environment: Three main depositional environments are recognized for the Chambira Fm. The conglomerates and sandbars observed in the lower term on the SW flank of the Maquía Anticline indicate the occurrence of channelized fluvial settings (Fig. 7C). The gray-blue clays topping the conglomeratic channel (CTA-32) in the NE flank would point to the coeval occurrence of a steady water pond (which is further supported by the crocodile and fish fauna; Fig. 7A-B; Supplementary Data). The blue clays of CTA-32 yield neither carbonized/lignitous wood nor pyrite nodules (contrary to what is observed throughout the Pebas Fm.). These channels are intercalated with distal floodplain deposits and paleosols, implying the preponderance of terra firme in the area, which is in turn consistent with the paleontological content as recorded in the concerned deposits (see above) and the presence of a fossil tree stump, found in-situ at the top of the Chambira Fm. (CTA-78; Figs. 3, 7D, S1).

No marine influence is recorded throughout the Chambira Fm. in the Contamana area, either based on sedimentology, ichnology, or paleontology (Supplementary Data; Table S3).

Correlation: The Chambira Fm. is also recognized in the NPFB and SPFB (e.g., Roddaz et al., 2010). Based on observations in the NPFB, Marocco et al. (1996) proposed that the deposits of the Chambira Fm. were ranging from the late Oligocene up to the middle Miocene, in fairly good agreement with our own observations.

3.1.4. Pebas Formation (late early to early late Miocene interval)

Description (Fig. 9): The Pebas Fm. is here for the first time recognized formally in the Ucayali Basin area, based on both sedimentological and paleontological arguments. Unambiguous Pebasian deposits crop out only in the SE flank of the Maquía Anticline and on the road to Agua Caliente (CTA-77; Figs. 1-2). The lowermost outcrop assigned to that formation (CTA-63; Figs. 2-3) consists of a 5 m-thick sequence with blue silts showing herringbone cross-bedding, covered by laminated blue clays with millimetric leaf litters and topped by a 2 m-thick blue clay, with pyrite nodules, lignitous wood and litter, and a rich vertebrate fauna. The Pebas sequence mainly comprises blue floodplain siltites and red paleosols, with scattered intercalated conglomeratic channels, rich in lignitous and/or pyritized floated wood (e.g. CTA-45, CTA-44, CTA-43, CTA-10, or CTA-75; Fig. 9). The corresponding section is coarsening upward (Fig. 3). In the SE flank of the Maquía Anticline, deposits of the Pebas Fm. crop out continuously between CTA-63 and CTA-75 (Fig. 2), with a measured thickness of 340 m (Figs. 3, S1), in good agreement with the "maximum thickness of ~500 m" proposed by Roddaz et al. (2010). Some carbonated levels crop out throughout the sequence (decimetric limestone nodules in CTA-45; mollusk-rich hardground in CTA-44 Base [Fig. 9B]; calcretes of diagenetic origin in CTA-75). The uppermost level is CTA-75

(Fig. 3), a sandy polygenic conglomeratic channel with a species-poor vertebrate and mollusk assemblage (Supplementary Data), topped by a calcrete-rich paleosol.

A 1 m-thick seismite, with sismoslumps, crops out in the upper part of the Pebas Fm. (~40 m above CTA-43 and 5 m below CTA-76), intercalated between low-energy whitish sandstones with trough cross-stratification.

Paleontological content (Fig. 10): In contrast to the underlying sediments of the Huchpayacu, Pozo, and Chambira formations, the fossil record of Pebasian deposits is much better documented at the Western Amazonian scale (e.g., Hoorn & Wesselingh, 2010; Salas-Gismondi et al., 2015). The Contamana area is no exception, with many diversified assemblages recovered, encompassing plant remains (essentially pollen and spores, but also floated wood, carbonized fruits and seeds), foraminifers, dinoflagellates, mollusks (inner moulds or shells preserved), crustaceans (ostracods and crabs), annelids and poriferans (CTA-58 and CTA-77), urchins (CTA-58), and species-rich vertebrate faunas (> 30 taxa in CTA-63, CTA-44 Top, and CTA-43; Supplementary Data).

The pollen and spore record is excellent, especially in CTA-44 Middle (130 taxa identified; see Table S3). The most characteristic palynological associations in the fluvial settings contained a wide variety of rainforest taxa including families Arecaceae, Melastomataceae, Sapotaceae, Euphorbiaceae, Leguminosae, Annonaceae, Meliaceae, Malvaceae and Malpighiaceae (Table S3). The most abundant taxa were those nearest to the aquatic depositional environment such as *Mauritia* (*Mauritiidites*), typical of palm swamps, accompanied by taxa from the fluvial overbanks such as *Amanoa (Retitrescolpites? irregularis)*, *Alchornea* (*Ranunculacidites operculatus*), and Malvaceae (including several Bombacoideae). The presence of aquatic (mostly freshwater) settings is supported by taxa such as the fern *Ceratopteris* (*Magnastriatites grandiosus*), a small aquatic fern bordering lakes and riverbanks (Germeraad et al., 1968) and freshwater algae *Botryococcus* and *Azolla*.

These fluvial/freshwater settings were occasionally disrupted by marine floodings, as suggested by sample CTA-44 Middle that has a moderate abundance of marine palynomorphs, including at least four species of dinoflagellate cysts (referred to as the genera *Spiniferites, Brigantedinium, Impletosphaeridium*, and *Trinovantenidium*), and chitinous foraminiferal test linings (Table S3), with a preservation similar to that from other Pebasian localities from Western Amazonia (see Boonstra et al., 2015). *Spiniferites* sp. was also recovered from CTA-58.

Microfossils were recovered in three localities (CTA-44 Middle, CTA-58, and CTA-77), all considered to be laterally equivalent and coinciding with the middle-late Miocene transition, based on both lithostratigraphical and paleontological proxies. Foraminiferan assemblages (poorly diversified: 4–21 co-occurring species; Fig. 10A-G) are dominated by *Ammonia beccarii* (up to 80% in terms of specimens; Fig. 10A) and widely homotaxic at the species level, especially between CTA-58 and CTA-77 (Simpson Index = 100) or CTA-44 and CTA-77 (Simpson Index = 50), to a lesser extent between CTA-44 and CTA-58 (Simpson Index = 25; Supplementary Data). Ostracod assemblages are dominated by Cytheroidea (with both cosmopolitan and endemic taxa; Fig. 10H-I). Calcareous algae and dinoflagellates are also characteristic for these levels. Foraminifers are strikingly reminiscent of those from Colombian Amazonia (e.g., Leticia, Puerto Nariño, Zaragoza and Macarena), whereas ostracods are mainly "Pebasian" (*sensu* Wesselingh et al., 2006).

Inframillimetric burrows and calcium carbonate tubes on oyster shells recovered in CTA-58 and CTA-77 attest to the presence of clionid demosponges and serpulid annelids, respectively.

Mollusks recovered from the Cachiyacu section are typical Pebasian endemics (*sensu* Wesselingh et al., 2006; Fig. 10R-T; Supplementary Data). Their alpha-diversity is low with respect to what is recorded at the Pebas Mega-Wetland scale (1–13 associated species in

CTA-44 Base *vs*. up to 95 co-occurring species in late middle Miocene localities around the city of Iquitos; Wesselingh et al., 2006, chap. 2). On the other hand, ostreid bivalves (*Crassostrea* sp., thousands of specimens found in-situ, with associated valves, in CTA-58 and CTA-77) are attested for the first time in Western Amazonia (Figs. 9D, 10R-S).

Crustaceans are documented by decapods (trichodactylid crabs, found only in the middle and upper members; Table S2) and Pebasian ostracod assemblages (CTA-58 and CTA-77, moderately diversified; Supplementary Data), the latter mostly consisting of representatives of the *Cyprideis* species flock (Fig. 10H-I; Wesselingh & Ramos, 2010; Gross et al., 2013). These ostracod faunas are remarkably similar to that of a middle Miocene core nearby the Rio Iutí, in Western Brazil, which also yielded bryozoans and barnacles (Linhares et al., 2011).

Urchin spines were found associated with foraminiferans and dinoflagellates in CTA-58. Vertebrates recovered from the Pebas Fm. in the Contamana area include selachians (stingrays, eagle rays, and sawfishes) and ray-finned fishes (mostly characiforms and siluriforms), but also a lepidosirenid lungfish (CTA-44 Top), sauropsids (snakes, lizards, crocodylomorphs, and turtles) and mammals.

Ichthyofauna is a conspicuous element of vertebrate assemblages in the concerned localities, with 10 to 13 co-occurring species (CTA-63, CTA-44 Top, CTA-43, and CTA-75; Supplementary Data). Most levels yield chondrichthyans (Fig. 10U-W), with a maximum diversity in CTA-44 Top (two potamotrygonids, a dasyatid, and a pristid) and CTA-43 (same association, plus a myliobatid; Supplementary Data). Actinopterygian faunas, strongly similar throughout the Pebas Fm., are dominated by large serrasalmine, cynodontid, and anostomid characiforms (pacus, piranhas, dogtooth characins, and headstanders, respectively) and, to a lesser extent, by small loricariid siluriforms (muffel-like teeth; Fig. 10X).

Pleurodirous chelonians are abundantly represented in terms of remains (shell fragments). They mostly consist of podocnemidid turtles (Table S2), but several keeled plates are likely to attest to the presence of chelids in CTA-63.

Squamate remains are either referable to snakes of uncertain affinities (vertebrae: CTA-43, CTA-75) or a durophagous lizard (teiid/tupinambid isolated tooth; CTA-63; Supplementary Data).

Crocodylomorph assemblages include up to four taxa, typically encompassing a gavialoid and one or two caimanines (*Caiman*, *Purussaurus*, and/or a durophagous species), but also a terrestrial sebecid (*Langstonia* sp.) in CTA-63 (Fig. 10K; Table S2). Such a composition is intermediate between what is observed in other Pebasian crocodylomorph hotspots such as the Fitzcarrald local fauna (Salas-Gismondi et al., 2007) and IQ-26/IQ-114 (nearby Iquitos, Peru; Salas-Gismondi et al., 2015).

Seven successive levels referred to the Pebas Fm. have yielded mammalian remains, and three of them are species-rich (12–16 co-occurring species in CTA-63, CTA-44 Top, and CTA-43; Supplementary Data). As usual in Miocene deposits from Western Amazonia (see Tejada-Lara et al., 2015), metatherian remains are rare and document a low taxonomic diversity (isolated teeth). They are represented by unidentified didelphimorphs (in CTA-63 and CTA-43; Fig. 10L), a marmosid didelphimorphian in CTA-43), a small sparassodont (CTA-44 Top), and an argyrolagid polydolopimorphian (CTA-43; Fig. 10Y-Z). Xenarthran specimens encompass cingulates, with *Parapropalaeohoplophorus* sp. in CTA-63 (Fig. 10M) and *Neoglyptatelus* sp. in CTA-43 (Fig. 10AA), pampatheriids (unidentified in CTA-63; cf. *Scirrotherium* sp. in CTA-44 Top and CTA-43; Fig. 10AB) and dasypodids (dasypodine in CTA-63; tolypeutine in CTA-44 Top; unidentified in CTA-43 and CTA-75) and a very few pilosan remains (Supplementary Data). Ground sloths, closely allied to *Pseudoprepotherium* and *Octodontobradys* from the middle Miocene of Colombia and late Miocene of Brazil (dos

Santos et al., 1993), occur in CTA-63 and CTA-57, respectively (isolated teeth eight-shaped in occlusal view, and a claw; Fig. 10AC-AD). A second phalanx of a small mylodontoid sloth was also unearthed in CTA-43.

Remains documenting native South American ungulates are rare, with only a distal tibia and a lower molar fragment assigned to litopterns (CTA-75) and a few isolated notoungulate teeth collected, either protohypsodont (?leontinid toxodont in CTA-63), or hypselodont (toxodontid in CTA-63 and CTA-44 Top; interatheriine interatheriid in CTA-57; Fig. 10AE). No indisputable astrapotheriid remains were found in-situ.

In contrast, rodents are the most abundant and diversified mammalian component (mostly isolated teeth) of vertebrate assemblages in the deposits of the Pebas Fm. (Fig. 10OQ, AF-AL). The concerned remains document all major groups, such as Octodontoidea and Chinchilloidea (from CTA-63 up to CTA-75), but also Cavioidea, and Erethizontoidea. Octodontoids encompass *Protadelphomys* sp. (CTA-63; Fig. 10O), a late representative of *Acarechimys* (CTA-43 and CTA-75; Fig. 10AF), and several taxa of unidentified affinities (Supplementary Data). Chinchilloids are more diversified among rodents (Fig. 10P-Q, AH-AL), with seven taxa occurring throughout the Pebas Fm. (CTA-63 / CTA-75), including Dinomyidae (e.g., low-crowned "*Scleromys*" in CTA-63; *Potamarchus* sp. in CTA-44 Top, CTA-43, and CTA-75; *Drytomomys* sp. in CTA-44 Top; eumegamyine in CTA-43; *Simplimus*? in CTA-57), and the neoepiblemid *Neoepiblema* sp. (CTA-44 Top and CTA-10). On the other hand, cavioids and erethizontoids are only observed in the upper part of the formation, with an unidentified dasyproctid (CTA-44 Top) and a new caviine (CTA-44 Top and CTA-43; Fig. 10AG), and the erethizontid *Steiromys*? sp. (CTA-43), respectively.

Bats are documented by an emballonurid in CTA-63 and CTA-75 (Fig. 10AM) and a molossid in CTA-44 Top (Supplementary Data). Isolated teeth of two new cebid primates (a medium-sized cebine and a tiny callithrichine) were recovered at CTA-43. No North

American immigrant was recognized in the deposits ascribed to the Pebas Fm. in the Contamana area (Supplementary Data), but a lower molar of an indisputable trichechid sirenian was unearthed in the lowermost level (CTA-63).

Age: Thirteen fossil-yielding localities in the Contamana area are assigned to the Pebas Fm. (Fig. 3; Tables 1, 3). They document at least eight successive levels in a single section (SW of the Maquia Anticline; Fig. S1), which can be gathered into four clusters (CTA-63 [early Miocene]; CTA-09 + CTA-45 [late early/early middle Miocene]; CTA-44 Base + CTA-44 Middle + CTA-58 + CTA-77 [middle/late Miocene transition]; CTA-44 Top + CTA-43 + CTA-58 + CTA-10 + CTA-76 + CTA-75 [early late Miocene]). These localities are distributed over a long stratigraphical interval, as they range from the early Miocene (Colhuehuapian-Santacrucian SALMAs; 20–17 Ma) up to the late Miocene (Mayoan/Chasicoan SALMAs; 11–9 Ma).

The early Miocene age of CTA-63 is mostly constrained by its rodent assemblage, with the octodontoid *Protadelphomys* sp. (Colhuehuapian SALMA; Vucetich & Bond, 2013; Arnal et al., 2014) and a relatively low-crowned dinomyid comparable to *Scleromys quadrangulatus* from Patagonia and Peruvian Amazonia (post-Colhuehuapian/pre-Santacrucian 'Pinturan' stage; Kramarz, 2006; Marivaux et al., 2012). The glyptodontid *Parapropalaehoplophorus* sp. was also restricted to the Santacrucian SALMA (Chucal Fm., Chile; Croft et al., 2007) before two osteoderms late middle Miocene in age were referred to as the same taxon by Tejada-Lara et al. (2015; Laventan SALMA, Fitzcarrald local fauna, Peru).

Contrary to the underlying localities CTA-09 and CTA-45, which are poorly age-constrained and assumed to be late early to middle Miocene in age (mainly based on their position in the section), CTA-44 has yielded three successive assemblages of high biostratigraphic interest. The mollusks of CTA-44 Base are latest middle Miocene in age (mollusk zone MZ8, ~12 Mya; Wesselingh et al., 2006), the microfossil assemblage of CTA-

44 Middle is most probably recording the middle-late Miocene transition (pollen and foraminiferans; Supplementary Data), and the mammalian fauna of CTA-44 Top documents the earliest late Miocene (Mayoan SALMA; rodents *Neoepiblema*, *Potamarchus*, and *Drytomomys*). Laterally equivalent localities, CTA-58 and CTA-77, yielded mollusks, Pebasian ostracods, and palynomorphs pointing to a similar age (middle-late Miocene transition; Fig. 2; Supplementary Data).

The species-rich locality CTA-43, located 24 m above CTA-44 Top in the same section, is most probably earliest late Miocene in age (Mayoan SALMA). There co-occur taxa of late middle Miocene affinities (Laventan SALMA; hypselodont argyrolagid marsupial: Sánchez-Villagra et al., 2000; *Steiromys*, *Acarechimys*, *Scirrotherium*, and *Neoglyptatelus*: Madden et al., 1997) and of late Miocene/Pliocene affinities (Chasicoan SALMA onward; eumegamyine rodents: Zárate et al., 2007; caviine cavioid: Pérez & Pol, 2012). A similar age is hypothesized for CTA-57. The uppermost localities ascribed to the Pebas Fm. (CTA-10, CTA-76, and CTA-75) are considered not to be significantly younger than CTA-43, as they notably include the same representatives of *Acarechimys* and *Potamarchus* as the latter locality (Fig. 10AF, AJ-AK; Supplementary Data), further supporting a high sedimentation rate for the concerned interval. The seismite level that is cropping out between CTA-43 and CTA-76 attests to a tectonic activity, suggesting that thrust tectonic movements were active by early late Miocene times, which is in agreement with data available for the Central Andes (Mora et al., 2010; Espurt et al., 2011; Armijo et al., 2015) and the northern Peruvian Subandean Zone (Eude et al., 2015).

Depositional environments: Blue clays with thin lignite seams and pyrite nodules (e.g., CTA-63 and CTA-44 Base; Fig. 9A) are strikingly reminiscent of early and middle Miocene fossiliferous deposits from the Pebas Fm. in the Iquitos area (e.g., Antoine et al., 2006; Wesselingh et al., 2006; Salas-Gismondi et al., 2015). Conversely, other fossil-yielding levels,

essentially consisting of unconsolidated and unsorted conglomerates and sandstones (e.g. CTA-45, CTA-44 Top, CTA-43, CT-76, or CTA-75) in the Cachiyacu section, are likely to document transgressive lags. They are much similar to the late middle Miocene Fitzcarrald bone beds in terms of organization and thickness (referred to the Ipururo Fm.; Fig. 1B; Espurt et al., 2007, 2010; Pujos et al., 2013; Tejada-Lara et al., 2015).

The laminated blue siltites with leaf litter in CTA-45 are particularly rich in organic matter. Environments may change drastically within a single outcrop (CTA-44, 10m-thick; Fig. 9A-C; Supplementary Data), with successive levels documenting (*i*) a lake shore (CTA-44 Base: mollusk assemblage within a carbonated hardground; Fig. 9B), (*ii*) a coastal plain with marginal marine affinities (CTA-44 Middle: pollen, foraminiferans, and dinoflagellate assemblage), (*iii*) a channelized estuarine embayment (CTA-44 Top: vertebrate assemblage with a mixture of terrestrial, riverine, and marine taxa; Fig. 9C), and (*iv*) a channel experiencing instant floodings as attested by the 3 m-thick topping conglomerate, with pluri-decimetric clay pebbles wrenched off from close upstream banks (Figs. 9A, S1). Similarly, in CTA-76 (Upper Member), a coarse conglomerate overlies a bivalve-rich bed within ochre sands showing an oblique stacking pattern typical of a unidirectional stream.

In CTA-58, 21 foraminiferan species co-occur, dominated by *Ammonia*, and ostracods of mesohaline-euryhaline affinities (e.g., *Perissocytheridea acuminata*, *Rhadinocytherura amazonensis*; Gross et al., 2013). The ostracod assemblage is strikingly reminiscent of that from a marine interval recognized in coeval deposits of Western Brazil (Solimoes Fm.; Linhares et al., 2011). The dinoflagellate *Spiniferites* sp. (CTA-44 and CTA-58) and unidentified urchins (spines; CTA-58) further attest to marine affinities. Accordingly, *Crassostrea* oysters from CTA-58 (Fig. 9D) and CTA-77 are perforated by clionid demosponges and covered by serpulid annelid tubes. One of them bears an imprint of a *Cerithium*-like gastropod (Fig. 10RS).

The top of the Pebas Fm. as observed in the SW flank of the Maquía Anticline is marked by calcrete-rich paleosols (CTA-75).

Correlation: The Pebas Fm. was formerly named in the Iquitos-Pebas area. It is correlated with the Solimoẽs Fm. in northwestern Brazil; in most recent works illustrating the PMWS, marine incursions and tectonic pulses are considered as major markers for intra-basin correlation between Peru, Brazil, Colombia, Ecuador, and Bolivia (Hoorn et al., 2010b; Roddaz et al., 2010; Boonstra et al., 2015; Salas-Gismondi et al., 2015).

3.1.5. Ipururo Formation (late Miocene–?early Pliocene)

Description: The Ipururo Fm. crops out extensively in the SW flank of the Maquía Anticline (Fig. 2), and along the tracks in the close outskirts of Contamana. The concerned deposits conformably overlie those of the Pebas Fm. They are dominated by more or less friable gray conglomerates and sandstones intercalated with yellowish and brown paleosols, and dominated by quartz, crystalline rock, and clay pebbles. These levels are strongly folded, with dips exceeding 45° downstream the Quebrada Cachiyacu and close to the Río Ucayali (Fig. 2), in accordance with the observation of Kummel (1948: 1258). Based on available surface data (exposures and dips), their total thickness may exceed 1,200 m. There is no exposure on the right bank of the Río Ucayali, at least in the Contamana area.

Paleontological content: The fossil record is so far very poor within the Ipururo Fm. in the Contamana area, with only two successive fossil-yielding localities recognized in the SW flank of the Maquía Anticline (Figs. 2, 3). The lowermost locality is CTA-42, located ~160m above CTA-75 (i.e., the uppermost level ascribed to the Pebas Fm.), in the same section. There, a freshwater trichodactylid crabs, a fish-eating longirostrine crocodylomorph, and an unidentified caiman co-occurred (Supplementary Data). A mandibular fragment of a small representative of *Caiman* was unearthed in CTA-59, ~200 m above CTA-42 (Figs. 2, 3).

Age: No direct age constraint is available for the Ipururo Fm. in Contamana. Nevertheless, as it conformably overlies Pebas deposits and exceeds 500 m in terms of thickness, it is likely to document a long late Neogene interval (late Miocene–?Pliocene). Additional proxies, however, are needed for a reliable age constraint.

Depositional environment: Sedimentological data and paleontological evidences suggest fluvial depositional environments, alternating with floodplains and paleosols throughout the Ipururo Fm. The lack of preservation of organic matter in the levels sampled for palynology (CTA-42, CTA-59, and CTA-70; Figs. 3, S1) could suggest a fully fluvial environment with seasonal fluctuation of the water level. The available data do not point to marine episodes in the Contamana area during the concerned time interval.

3.1.6. Ucayali Formation (?late Pliocene–Pleistocene)

We have not thoroughly investigated the Ucayali Fm., i.e., the uppermost formation cropping out along the right bank of the Río Ucayali in the Contamana region, neither from a paleontological perspective nor for stratigraphy. The corresponding fluvio-lacustrine settings form horizontal terraces unconformably overlying deposits of the Ipururo Fm. (Fig. 2; Kummel, 1948). Their hypothesized thickness does not exceed 75m, which coincides with the height of the highest terraces, SE to Contamana (Fig. 2). To our knowledge, no fossil content was described in the concerned deposits, except for some vertebrate specimens unearthed in a remote area of the Ucayali Basin (Río Pachitea; Spillman, 1949). Besides, the field-based description by Kummel (1948), a recent review of the concerned unit and equivalent formations (e.g., Marañon Fm.) at the Western Amazonian scale is available in Roddaz et al. (2010).

4. Discussion

4.1. Taxonomic diversity trends (Eocene–Miocene)

The overall taxonomic diversity in the Contamana section and its evolution throughout the Eocene–Miocene interval (excluding palynomorphs) are depicted in Figure 11 at the class/infraclass, order, family, and species levels. The time intervals considered coincide with well-diversified fossil-yielding locality clusters, i.e. the middle Eocene (Pozo Fm., Lower Member), the late Oligocene (Chambira Fm., Lower Member), the early Miocene (Pebas Fm., Lower Member), the middle Miocene (Pebas Fm., Middle Member; somewhat biased by a poor fossil record regarding vertebrates), and the late Miocene (Pebas Fm., Upper Member + Ipururo Fm.). We have chosen not to include the Paleocene Huchpayacu Fm., as its fossil record is both virtually undocumented and presumably highly biased (CTA-54, charophyte-dominated; Supplementary Data).

As illustrated in Fig. 11b, the middle Eocene, late Oligocene, early Miocene, middle Miocene, and late Miocene assemblages display a fairly constant higher-level taxonomic diversity throughout the period documented (ranging from 8 to 12 classes or infraclasses; Supplementary Data). Order-level diversity fluctuates to a greater degree, with a decline in the early and middle Miocene (15 and 17 co-occurring orders, respectively) compared to earlier intervals (28 in the middle Eocene; 23 in the late Oligocene) and the late Miocene (20 co-occurring orders; Fig. 11c). Nevertheless, this first-order analysis does not take into account the replacement of terrestrial vertebrates by aquatic organisms with marine or fluvio-lacustrine affinities in the “Pebasian” interval (early and middle Miocene). In other words, overall diversity might be comparable but with strikingly distinct components: non-vertebrate taxa of marine affinities during the early and middle Miocene interval (PMWS: dinoflagellates, foraminiferans, most ostracods, serpulid polychetes, ostreids, and

demosponges; Supplementary Data) as opposed to a vertebrate-dominated biota during earlier and later intervals (Fig. 11b-e; Table S2).

At the family/species level, the richest interval is the middle Eocene one with 59/92 co-occurring taxa. This huge diversity is maintained during the late Oligocene (56 families encompassing 73 species), but with a stronger vertebrate component (Fig. 11d-e). The lowest family/species diversity (32/38) is recorded during the early Miocene. The drastic drop in species/family diversity recorded then might result from the coincidence of at least two factors: (i) a sustainable environmental change occurred at regional scale with the onset of the lacustrine-dominated Pebas Mega-Wetland System. The latter replaced fully fluvial-dominated conditions prevailing until then, which most likely affected both the aquatic and terrestrial components of the ecosystems (Wesselingh et al., 2006; Hoorn et al., 2010; this work); (ii) there is an obligate sampling bias, as the early Miocene interval comprises only one species-rich locality in our analysis (CTA-63) whereas we have grouped CTA-09 and CTA-45 (of uncertain age: late early or early middle Miocene) with unequivocal middle Miocene localities (CTA-44 Base, CTA-44 Middle, CTA-58, and CTA-77; Supplementary Data). By contrast, the middle and late Miocene intervals document increasing diversity with 44 and 46 co-occurring families, respectively. Species-richness is higher during the middle Miocene (76) than the late Miocene (60), due to the occurrence of polytypic/plurispecific ostracod and foraminiferan genera in the former interval (Fig. 11a,e). In general, overall family- and-species diversity declines throughout the concerned interval, with a drastic drop in the early Miocene (32 families/38 species). This compares with 59/92 and 56/73 in earlier Paleogene time slices and 44/76 and 46/60 taxa in later time slices (middle and late Miocene, respectively; see Supplementary Data).

From a taxonomic perspective, charophytes only occur in the early Paleocene + middle Eocene interval, with a comparable diversity (13–14 species; Table 2; Fig. 11b).

Trichodactylids are abundant in all intervals except the early and middle Miocene (absent). Chondrichthyes increase in diversity through time: only freshwater potamotrygonids are present during the Paleogene interval, whereas dasyatids, myliobatids, and pristids (of marine affinities) occur in all Miocene time slices (along with potamotrygonids; Fig. 11d-e). The actinopterygian ichthyofauna (mainly characiforms and siluriforms) is relatively invariant throughout the concerned interval in terms of taxonomic content (Fig. 11c-e), in contrast to the highly fluctuating chondrichthyan component. However, no siluriform has yet been recorded from the early Miocene. Dipnoi are only recognized in the late Miocene period (CTA-44).

The amphibian (anuran) record in the Contamana area is restricted to the Paleogene interval (Supplementary Data; Fig. 11b-e): no Neogene representative has been unearthed so far.

Chelonia and Lepidosauria are not identified precisely enough to allow for a significant interpretation in terms of diversity trends. Crocodylomorphs are a consistent component of Contamana assemblages at any taxonomic level (Fig. 11b-e), with a sebecid (closely allied to either *Sebecus* in Paleogene localities or *Langstonia* in Miocene ones), caimanines (generalist and/or malacophagous), and gharials co-occurring in most cases.

In general, mammalian diversity appears to have reached a climax during Paleogene times in the Contamana area (Fig. 11), with 14/28/44 middle Eocene and 11/29/38 late Oligocene orders/families/species, compared with 7/14/15 early Miocene, 1/2/2 middle Miocene, and 9/23/28 late Miocene co-occurring orders/families/species. Even taking into account that the early and middle Miocene interval is likely under-sampled, the late Miocene mammalian assemblage is impoverished with respect to its Paleogene counterpart, as many endemic taxa had apparently disappeared by that time, and northern GABI-induced immigrants have not yet been documented. In particular, potential allotherians (?sudamericid gondwanatheres) are

restricted to the earliest interval (middle Eocene; Supplementary Data). Similarly, Metatheria are well-represented and widely diversified in Paleogene localities (5/4 co-occurring orders, 7/8 families, and 15/9 species in the middle Eocene/late Oligocene, respectively), whereas they are much rarer (zero to four species) in Miocene assemblages (Fig. 11b-e; Supplementary Data). Xenarthrans are never abundant, and their taxonomic diversity does not vary throughout the documented range. Cingulates are dominant over sloths (but this may be a taphonomic bias as the former are only documented by osteoderms; Gaudin & Croft, 2015). Three cingulate families co-occur with mylodontoid sloths from the late Oligocene onward. Among South American native ungulates, notoungulates are by far the most diversified in Contamana localities, with a family/species diversity decreasing abruptly at the Oligocene-Miocene transition. Both the 'trigonostylopid' astrapothere and pyrotheres are restricted to the earliest documented interval (middle Eocene), in good agreement with their record at the South American scale (e.g., Kramarz et al., 2011).

Rodents provide a much better sketch in both a taxonomic and biostratigraphic perspective. There is no common taxon between the middle Eocene and the late Oligocene assemblages (stem caviomorphs *vs*. representatives of Recent superfamilies), whereas a relative continuity is observed between the late Oligocene and the early Miocene. Dinomyids characterize Neogene localities at Contamana, in agreement with both the Argentinian and Brazilian fossil records (e.g., Kerber et al., 2015). Their generic diversity increases throughout the Miocene interval. Dasyproctidae and Neoepiblemidae are only documented in late Miocene localities. Bats are rare but do occur throughout the documented period, except during the under-sampled middle Miocene interval (absent), with up to three co-occurring families and species. Two intervals have yielded primates (late Oligocene, late Miocene) with two species recorded in both cases (Supplementary Data). A single trichechid sirenian specimen was identified throughout the documented section (Pebasian interval).

4.2. Paleoenvironmental inferences

4.2.1. Depositional environments

Based on the observations of the previous section, depositional environments can basically be grouped in three distinct clusters:

- (*i*) fluvial settings, testifying to the occurrence of depositional environments highly comparable to the recent ones of the Quebrada Cachiyacu;
- (*ii*) lacustrine settings (oxbow lakes or piranha-rich "cochas");
- (*iii*) bay margin/coastal settings (blue clays with lignitic seams and a mixture of fossil remains of terrestrial, freshwater, and marine affinities; transgressive lags).

Together with lithology in general, mollusks, ostracods, and charophytes are the best markers for defining the geological formations in the Contamana area:

- Lower Huchpayacu Fm.: carbonates that preserve numerous charophytes but almost no mollusks and no palynomorph; dysoxic lacustrine environments;
- Pozo Fm. ('Pozo Sands'): sedimentation dominated by floodplain deposits transformed into variegated paleosols intercalated with channelized fluvial sandstones; diagenetic millimetric carbonate nodules are preserved, with numerous palynomorphs, (secondarily silicified) charophyte oogonia, ostracods, and mollusks (inner casts – no shell preserved);
- Chambira Fm.: sedimentation dominated by polygenic conglomerate channels and floodplain deposits, transformed into red paleosols with anhydrite veins; no carbonates, palynomorphs, charophytes, ostracods, or mollusks are preserved;
- Pebas Fm.: sedimentation dominated by red-grayish paleosols and blue clays (with pyrite nodules and lignitous lenses); carbonates may occur (nodules and hardgrounds);

mollusks are abundant and diversified (shells preserved; bivalves + gastropods); palynomorphs are diverse and well-preserved; foraminiferans, dinoflagellates, and brackish to marine ostracods are abundant; no charophytes preserved, except in one locality;

- Ipururo Fm. + Ucayali Fm.: sedimentation dominated by coarser deposits (conglomerates intercalated with sandstones and siltstones) rather than floodplain deposits); no carbonates, palynomorphs, charophytes, mollusks, or ostracods.

4.2.2 Paleoenvironments as inferred by organisms

Based on recent biomes, consensual inferences regarding fossil organisms recovered, and lithology (Table S4), we have considered ten hypothetical biotopes *a priori*, either terrestrial (high-elevation range, savanna, rainforest), aquatic (freshwater: lake/pond, river/small stream; brackish: delta/estuary, coastal plain; marine: inner shelf), or at the interface between two of them (floodplain, mangrove). This allows for sketching landscape evolution in Contamana during the Cenozoic.

The Contamana area was fully dominated by freshwater environments within a tropical rainforest throughout the concerned period (Table S4): primarily rivers and small streams (early Paleocene–Recent), but also lakes (early Paleocene; late Oligocene; Miocene). Floodplains are inferred from the occurrence of "terrestrial" crocodiles (sebecids) and tree stumps (middle Eocene; late Oligocene; early Miocene) in fine-grained paleosols. There is no clue for any high-elevation (Andean), mangrove, or open terrestrial habitats (savanna or "chaco"), at least from the palynological record (Tables S3-S4). Although other biotic components consistently point to a tropical rainforest (with brackish/marine inputs; Table S4), the co-occurrence of mammals with ever-growing teeth, such as argyrolagid marsupials or dinomyid and caviine rodents, indicates a higher rate of abrasive food (dust/ashes) at the end

of the Pebasian interval (CTA-44 Top and CTA-43; early late Miocene). Marine influence is suggested during the middle Eocene (coastal plain/marginal marine: dinoflagellates in CTA-47; ostracod in CTA-27) and strongly evidenced during the middle Miocene (CTA-45: brackish water rays) and around the middle-late Miocene transition (co-occurrence of a wide array of marine organisms in CTA-44 Middle, CTA-58, and CTA-77; Table S4).

4.2.3. Correlation with other Amazonian sub-basins

A marine corridor bordered the eastern flank of the Proto-Andes during the late Cretaceous, as shown extensively from Argentina to Colombia (e.g., Lundberg et al., 1998; Hoorn et al., 2010a; Louterbach et al., 2014). Accordingly, marine deposits are recorded in the NPFB (Lundberg et al., 1998), SPFB (based on selachian ichthyofauna; Louterbach et al., 2014), and Ucayali basin (Kummel, 1948). It seems that this shallow seaway withdrew around the Cretaceous/Paleogene transition (Lundberg et al., 1998), which is supported by the early Paleocene record of the Contamana area (Huchpayacu Fm., base; Fig. 12). Unfortunately, the present study provides no data for the middle Paleocene–early Eocene interval; although tidal sands assigned to the Casa Blanca Fm. (and thus coinciding with the corresponding interval; Fig. 12) are cropping out in other parts of the Ucayali Basin (Pachitea; Kummel, 1948), it is so far impossible to test whether a connection existed with either the NPFB (Paleocene continental and Eocene marine-dominated sedimentation; Roddaz et al., 2010) or the SPFB (late Paleocene marine incursion; e.g., Louterbach et al., 2014). Conversely, independent sub-basin dynamics between the NPFB and the Ucayali Basin can be assumed during the middle Eocene (well-documented and time-constrained in Contamana), and perhaps the late Eocene as well (Fig. 12). By late Oligocene and earliest Miocene times, sedimentation seems to have been homogenous throughout Peruvian lowlands and Subandean zones, with the fluvial-dominated Chambira deposits. The PMWS subsequently developed in both the NPFB and the Ucayali Basin between the late early and early late Miocene (Fig. 12; Antoine et al., 2013). At

least from a paleontological perspective, no Pebasian influence is recorded in the SPFB, as the southernmost assemblage of ascertained Pebasian affinities was mentioned at Sepahua on the Río Urubamba (middle Miocene mollusks, 11° 10’ S; Wesselingh et al., 2006). An early late Miocene marine incursion is recorded throughout the NPFB and Ucayali Basin (Fig. 12; Boonstra et al., 2015 and this work), testifying to a single event, perhaps distinct from the later one(s) documented in the SPFB (e.g., Hovikoski et al., 2010). From Pliocene times onward (initiated at ~4 Ma; Espurt et al., 2007; Roddaz et al., 2010), the Fitzcarrald Arch was uplifted as a pivotal topographic high at the Western Amazonian scale, which may explain the discrepancies between the Ucayali basin, connected with the NPFB, and the Madre de Dios basin (SPFB).

4.3. Paleobiogeography

The fossil assemblages documented in the Paleocene–?Pliocene interval in the Contamana area attest at least to four biogeographic histories, sometimes interwoven and inherited from (*i*) Mesozoic Gondwanan times, (*ii*) the Panamerican realm prior to (*iii*) South America’s Cenozoic “splendid isolation”, and (*iv*) Neotropical ecosystems in the Americas.

4.3.1. Gondwanan faunal and floral components

Aquatic taxa are the most conspicuous biotic elements of Gondwanan affinities in the Contamana section (charophytes, neritid gastropods and hyriid bivalves, cichlid actinopterygians, lepidosireniform lungfishes, plus chelid and podocnemidid turtles), in agreement with the conclusions of Brito et al. (2007) and Sterli & de la Fuente (2013). Similarly, pipid anurans occur only in South America and Africa (recent: San Mauro et al., 2005; fossil: Rage et al., 2013). Specimens assigned to that family are relatively common in

middle Eocene assemblages of the Contamana area, whereas no post-Eocene remains have been discovered so far (Supplementary Data).

Some terrestrial mammals, such as polydolopimorphian and microbiotherian marsupials, also attest to a Gondwanan legacy (also recorded in Australia and Antarctica; e.g., Archer et al., 1999; Goin et al., 1999, 2007; Sigé et al., 2009).

4.3.2. Panamerican heritage (and Holarctic outliers)

The Contamana Paleogene record supports a latest Cretaceous–early Cenozoic North American pathway for aquatic/freshwater taxa, such as corbulid bivalves (*Pachydon* group), freshwater stingrays (Potamotrygonidae; Table S2), and crocodylomorphs (durophagous caimanines), as already mentioned by Adnet et al. (2014) and Salas-Gismondi et al. (2015), and supported by geological evidence in Northern South America (Cardona et al., 2010, Bayona et al., 2011). The fact that interchanges between South and North America involved freshwater animals confirms that a continuous, well established terrestrial connection linked the two continents at that time (Gayet et al., 1992). The occurrence of possible herpetotheriid metatherians, of Holarctic/North American affinities in the late middle Eocene of Contamana (Supplementary Data), further supports the hypothesis of a terrestrial connection between these landmasses during the same interval (see also Goin & Candela, 2004; Sánchez-Villagra et al., 2007). Likewise, recent collagen-based phylogenetic studies point to close relationships of litopterns and notoungulates with Perissodactyla among Laurasiatheria, of undisputed Holarctic affinities, with a split around the Cretaceous-Paleogene transition (Buckley, 2015; Welker et al., 2015).

If confirmed, the presence of a probable rhinolophoid microchiropteran bat in the late Oligocene of Contamana (CTA-32; Supplementary Data) would considerably expand the geographic range of the superfamily, so far restricted to the Old World (Ravel et al., 2014),

though clearly the dispersal ability of bats is in no way comparable to that of scansorial or freshwater organisms (Calderón-Patrón et al., 2013).

4.3.3. South American endemics

Other components of the freshwater ichthyofauna recovered in Contamana, such as Potamotrygonidae *sensu stricto*, anostomid characiforms, and lepidosirenids, have a biogeographical history restricted to South America (Sidlauskas et al., 2008; Albert & Reis, 2011; Adnet et al., 2014). Also trichodactylid freshwater crabs are considered as autochthonous South American faunal elements (Klaus et al., 2011). The anilioid squamate from CTA-27 and sebecid mesoeucrocodylians have a similar range (Pol & Powell, 2011; Wallach et al., 2014). The mammalian fauna from the Contamana series also has a strong South American signature, with bonapartherioid and argyrolagid polydolopimorphians, paucituberculatans, and sparassodonts (e.g., Beck, 2012), but also South American native ungulates, such as pyrotheres and astrapotheres – possibly closely related to notungulates though (Billet, 2010) and, as such, to perissodactyls (Buckley, 2015; Welker et al., 2015). South American endemics are recorded as early as the middle Eocene in the Contamana area.

Our results are consistent with most recent paleogeographical maps for middle-late Miocene times (Antoine et al., 2013; Boonstra et al., 2015; Salas-Gismondi et al., 2015) in showing that the Contamana area was unambiguously part of the PMWS during a long interval (late early to early late Miocene). In particular, most ostracods, mollusks, and crocodylomorphs found in Contamana are Pebasian endemics (Wesselingh & Ramos, 2010; Salas-Gismondi et al., 2015).

4.3.4. Neotropical markers – no evidence for the Great American Biotic Interchange

Most actinopterygian clades documented in Contamana (serrasalmine, cynodontid, and erythrinid characiforms, but also loricariid and pimelodid siluriforms; Albert & Reis, 2011) have a South American Neotropical distribution today. Due to the closure of the Central American seaway in the Pliocene or perhaps even in Miocene times as suggested by Bacon et al. (2015) and Montes et al. (2015), these groups have subsequently dispersed into Central and North America. A similar scenario might be hypothesized for teiid lizards (Pujos et al., 2009), caimanine crocodylians (Salas-Gismondi et al., 2015), didelphimorphian marsupials (Sánchez-Villagra et al., 2007), and notoungulates (MacFadden, 2006). The xenarthran, caviomorph and platyrrhine biogeographic history appears to be much more complicated, with a South American differentiation and several subsequent dispersals to Caribbean islands, Central America, and/or North America during the Oligocene–Pleistocene interval (MacFadden, 2006; Antoine et al., 2012; Vélez-Juarbe et al., 2014).

Trichechid sirenians are fully aquatic and their fossil record encompasses both the Paleotropics and the Neotropics (e.g., Vélez-Juarbe, 2014). Nevertheless, the recognition of an early Miocene trichechine in the Cachiyacu section (CTA-63) supports the hypothesis of a Neotropical origin for manatees (e.g., Domning, 2005; Vélez-Juarbe, 2014). This record also pushes the presence of trichechines in South America from the middle Miocene (Domning, 1982) back to the early Miocene, implying that the group may have a more complex evolutionary history on the continent.

Conversely, based on the available samples, we have not documented direct evidence for North American terrestrial immigrants into the tropical rainforests of Peruvian Amazonia during the Miocene interval in Contamana that could coincide with an early onset of the Great American Biotic Interchange during the middle or late Miocene (Supplementary Data; Carrillo et al., 2014).

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Jules Chabain recently obtained an MSc degree in Paleontology at the University of Montpellier, France. His works focus on taxonomy, evolution, and diversity of the Cenozoic ichthyofauna from Western Amazonia. His main interests are palaeoecology, zoology, and geology.

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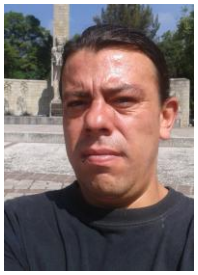

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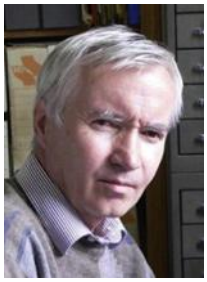
François Pujos is has received a PhD degree from the National Museum of Natural History of Paris. He is a former Researcher of the French Institute of Andean Studies and currently Researcher of the Argentinean Scientific and Technical National Research Councilin Mendoza. As a paleontologist focusing in systematics and evolution of South American Cenozoic mammals (e.g., Xenarthra), he has organized 25 field missions in South America and described new taxa, including several ground sloths. As a member of multidisciplinary teams, he has participated in the discovery of several new vertebrate communities from the Bolivian Altiplano and Peruvian Amazonia.



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Frank P. Wesselingh is Senior Researcher with scientific curatorial responsibilities at Naturalis, Leiden, Netherlands. After a study in Earth Sciences at the Vrije Universiteit Amsterdam, he continued as a curator (later researcher) at Naturalis. At the same time he engaged in a PhD on Amazonian landscape and biota during the Neogene at the Biology faculty, Turku University, Finland. He tries to document and understand the drivers behind biodiversity changes in the geological past, especially the role of changing landscapes in driving community and biodiversity change, mostly focusing on mollusks from Indonesia, the North Sea, or the Pontocaspian region.

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Figure and Table captions

Fig. 1. A: Location map of the main South American vertebrate-yielding Cenozoic localities mentioned in the text. B: Location map of Cenozoic profiles in the Contamana area, Peruvian Amazonia.

Fig. 2. Geological map of the Contamana area, Peruvian Amazonia. The CTA-54 locality (Huchpayacu Formation; early Paleocene) is out of the map: for location purpose, refer to Fig. 1B. Modified from Lipa et al. (1997).

Fig. 3. Synthetic section of Cenozoic deposits in the Contamana area, Peruvian Amazonia. See Fig. S1 for more information on hypotheses for correlation.

Fig. 4. Charophyte gyrogonites from the Huchpayacu Formation, Contamana, Peruvian Amazonia. CTA-54 locality, Agua Caliente section (early Paleocene; Fig. 1B). A: *Chara* "*Grambastichara*" *subcylindrica*, in lateral view. B: *Sphaerochara inconspicua*, in lateral view. C-E: *Sphaerochara huaroensis*, in lateral (C), apical (D), and basal views (E). F-H: *Nitellopsis supraplana sulcata*, in lateral (F), apical (G), and basal views (H). I-J: *Nitellopsis* (*Tectochara*) *merianii* in lateral (I) and basal views (J). K-M: *Peckisphaera* cf. *portezueloensis* / *Peckichara* sp., in lateral (K), apical (L), and basal views (M). N: *Peckichara* cf. *varians*, in lateral view. Scale bars = 500 µm.

Fig. 5. Pozo Fm., Lower Member ('Pozo Sands') at Contamana, Peruvian Amazonia. A: CTA-47 locality, with the Quebrada Cachiyacu at the foreground. B: CTA-27 locality. C:

Biotite and feldspar-yielding tuff dated 43.44±2.5 Ma at CTA-29. D: Carbonated nodule-rich sandy clays at CTA-66.

Fig. 6. Selected fossils from the Lower Pozo Formation, Contamana, Peruvian Amazonia. Quebrada Cachiyacu section (late middle Eocene localities). A-F: Charophyte gyrogonites: A: *Nodosochara jerbae*, in lateral view (CTA-47 locality); B-D: *Raskyella pecki meridionale*, in lateral (B; CTA-66 locality), apical (C; CTA-51 locality), and basal views (D; CTA-51 locality); E-F: *Stephanochara acris*, CTA-27 locality, in lateral (E) and apical views (F). G-H: Ostracoda: G: *Neocyprideis apostolescui*, left valve in lateral view (CTA-27); H: *Ilyocypris* aff. *lusitanica*, left valve in lateral view (CTA-27). I: Decapoda: trichodactylid crab claw (MUSM 2264; CTA-27). J-K: Gastropoda: J, unidentified pachychilid, in front view (MUSM 2265; CTA-27); K: *Charadreon* sp., in rear view (MUSM 2266; CTA-41). L-N: Actinopterygii: L, ?*Colossoma*, tooth in buccal view (MUSM 2267; CTA-27); M: *Leporinus* sp., tooth in palatine view (MUSM 2268; CTA-27). N: cf. *Hydrolycus* (MUSM 2269; CTA-27). O, Sebecosuchia: cf. *Sebecus*, tooth in lateral view (MUSM 1959; CTA-47). P-Q, Eusuchia: P: unidentified gavialoid tooth (MUSM 2270; CTA-27); Q: unidentified durophagous caimanine tooth (MUSM 2271; CTA-27). R: Metatheria: *Rumiodon* sp., left M2 in occlusal view (MUSM 2272;CTA-27). S-Z: Marsupialia: S-V: *Wamradolops* sp. (CTA-27). S, left P3 in occlusal view (MUSM 2273); T: right M1, in occlusal view (MUSM 2554); U-V: right hemimandible with p3-m2 and alveoli of m3 in lingual (U) and occlusal views (V) (MUSM 2555); W-X: *Sasawatsu* sp. (CTA-27). W, right M3 in occlusal view (MUSM 2556); X: right m3 in occlusal view (MUSM 2557); Y-Z: cf. *Perulestes* sp. 2 (MUSM 2558; CTA-27), right M2 in occlusal (Y) and linguo-occlusal view (Z). AA-AB: Xenarthra, Cingulata: AA, *Stegosimpsonia* sp., osteoderm in dorsal view (MUSM 2559; CTA-66); AB: *Eocoleophorus glyptodontoides*, osteoderm in dorsal view (MUSM 1586; CTA-29). AC:

Pyrotheria: cf. *Griphodon*, enamel fragment in lateral view (MUSM 2560; CTA-27). AD-AE: Notoungulata (CTA-27): AD: "*Eohyrax-Pseudhyrax-Punahyrax*", right p3-4, fragmentary, in occlusal view (MUSM 2561); AE: Unidentified interatheriid or "archaeohyracid", left upper cheek tooth fragment with closed fossette in occlusal view (MUSM 2562). AF: Rodentia: *Cachiyacuy* cf. *contamanensis*, right M2 in occlusal view (MUSM 2563; CTA-29). Scale bars = 500 µm (A-H, S-T, W-X), 1 mm (R, U-V, Y-Z, AD, AF), 2 mm (J-N, Q, AA, AC, AE), 5 mm (I), 10 mm (O, AB).

Fig. 7. Chambira Fm. at Contamana, Peruvian Amazonia. A: CTA-32 locality in 2008. B: Detail of fossiliferous blue microconglomerate and clays in CTA-32. C: Conglomerates with clay and metamorphic rock pebbles at the base of the Chambira Fm. (CTA-61 locality). Note the large turtle plate (black rectangle). D: Carbonized tree stump in life position, at the top of the Chambira Fm. (CTA-78).

Fig. 8. Selected fossils from the Chambira Formation, Quebrada Cachiyacu section, Contamana, Peruvian Amazonia (late Oligocene localities). A: Actinopterygii: piranha-like serrasalmine, anterior tooth in buccal view (MUSM 2564; CTA-32). B: Eusuchia: unidentified gavialoid tooth, in lateral view (MUSM 2565; CTA-32). C: Metatheria: ?Herpetotheriidae, left ?M1 in occlusal view (MUSM 2566; CTA-32). D-E: Marsupialia: D: *Abderites* sp., left M2 in occlusal view (MUSM 2567; CTA-32). E: cf. *Abderites*, left M2 in occlusal view (MUSM 2568; CTA-32). F-H: Xenarthra: F, unidentified pampatheriid, fragmentary osteoderm in dorsal view (MUSM 2569; CTA-32). G-H: unidentified mylodontid, fragmentary molariform in lateral (G) and occlusal views (H) (MUSM 2570; CTA-61). I-K: Notoungulata: I-J: unidentified interatheriine, left M1/2 in occlusal (I) and lingual views (J) (MUSM 2571; CTA-61). K: unidentified hegetotheriid-archaeohyracid,

fragment of a left upper cheek tooth in occlusal view (MUSM 2572; CTA-61). L-N: Rodentia: L: cf. *Eoincamys*, right m1/2 in occlusal view (MUSM 2573; CTA-61). M: *Deseadomys* sp., left M2, in occlusal view (MUSM 2574; CTA-61). N: cf. *Eosallamys*, right M2 in occlusal view (MUSM 2575; CTA-32). O: Chiroptera: unidentified emballonurid, lower canine, in lingual view (MUSM 2576; CTA-32). P-R: Primates: unidentified anthropoid, pollical phalanx in proximal (P), lateral (Q) and dorsal views (R) (MUSM 2577; CTA-32). Scale bar = 1 mm (A, C-E, L-R), 2 mm (B, I-K), and 5 mm (F-H).

Fig. 9. Pebas Fm. at Contamana, Peruvian Amazonia. A: CTA-44 locality, general view of CTA-44, showing CTA Base, CTA Middle, and CTA-44 Top. Black open rectangle denotes the bioturbated hardground as detailed in B (topping CTA-44 Base). White open rectangle denotes a conglomerate with micro- and macro-vertebrates detailed in C (transgressive base of CTA-44 Top). B: Bioturbated calcareous hardground at the top of CTA-44 Base, a mollusk-yielding level (see Supplementary Data). C: Detail of CTA-44 Top conglomerate, with the tip of a *Purussaurus* tooth cropping out in-situ. D: Detail of the oyster-rich level in CTA-58. Note that the individuals of *Crassostrea* have their valves paired and connected.

Fig. 10. Selected fossils from the Pebas Formation, Quebrada Cachiyacu section, Contamana, Peruvian Amazonia (late early to early late Miocene). A-I: Microfossils of marine affinities (CTA-58, Pebas Fm., Middle Member; middle-late Miocene transition). A-G: Foraminifera. A: *Ammonia beccarii* in umbilical view. B: *Protelphidium granosum* in dorsal view. C: *Holmanella valmonteensis* in umbilical view. D: *Rosalina californica* in umbilical view. E: *Anomalinoides salinasensis* in umbilical view. F: *Miliammina fusca* in umbilical view. G: *Bathysiphon* sp. in lateral view. H-I: Ostracoda. H: *Cyprideis* sp., left valve in lateral view. I: *Cyprideis amazonica*, left valve in lateral view. J-S: early Miocene vertebrates (CTA-63;

Pebas Fm., Lower Member). J: Actinopterygii: unidentified serrasalmine, oral tooth in occlusal view (MUSM 2578). K: Sebecosuchia: *Langstonia* sp., tooth in lateral view (MUSM 2579). L: Marsupialia: unidentified didelphimorph (sp. 4), right M2/3 in occlusal view (MUSM 2580). M-N: Xenarthra. M: *Prapropalaehoplophorus* sp., osteoderm in dorsal view (MUSM 2581). N: unidentified pampatheriid, marginal osteoderm in dorsal view (MUSM 2582). O-Q: Rodentia: O, *Protadelphomys* sp., left P4 in occlusal view (MUSM 2583). P-Q, "*Scleromys*" sp., right p4 in occlusal (P) and labial views (Q) (MUSM 2584). R-S, Mollusca (CTA-58, Pebas Fm., Middle Member; middle-late Miocene transition): *Crassostrea* sp., shell in lateral (R) and upper views (S) (MUSM 2585). Black arrow indicates imprint of a *Cerithium*-like snail in the oyster shell. T-AM: Late Miocene fossil specimens (Pebas Fm., Upper Member). T: Mollusca: *Pachydon cuneatus*, right valve from a pair, in lateral view (MUSM 2586; CTA-43). U-W: Chondrichthyes: U-V, *Rhinoptera* sp., palatine tooth in radical (U) and occlusal views (V) (MUSM 2587; CTA-43). W: *Pristis* sp., rostral tooth of juvenile individual, in vertical view (MUSM 2588; CTA-75). X: Actinopterygii, Siluriformes: unidentified loricariid, muffel-shaped tooth in palatine view (MUSM 2589; CTA-43). Y-Z: Marsupialia: Argyrolagidae, gen. et sp. indet., left m2/3 in occlusal (Y) and labial views (Z) (MUSM 2590; CTA-43). AA-AD: Xenarthra. AA: *Neoglyptatelus* sp., pentagonal osteoderm, in dorsal view (MUSM 2591; CTA-43). AB: cf. *Scirrotherium* sp., fragmentary semi-mobile osteoderm in dorsal view (MUSM 2592; CTA-43). AC-AD: *Octodontobradys* sp., molariform in occlusal (AC) and lateral views (AD) (MUSM 1949; CTA-57). AE: Notoungulata: unidentified interatheriine, fragmentary left P4 in occlusal view (MUSM 2593; CTA-57). AF-AL: Rodentia: AF, *Acarechimys* sp., left M1/2 in occlusal view (MUSM 2594; CTA-75). AG: unidentified caviine, right M1/2 in occlusal view (MUSM 2595; CTA-44). AH-AI, *Neoepiblema* sp., left p4 in occlusal (AH) and lingual views (AI) (MUSM 2596; CTA-44); AJ-AK, *Potamarchus* sp., left m1/2 in occlusal (AJ) and labial views (AK) (MUSM 2597;

CTA-44). AL: *Drytomomys* sp., right p4 in occlusal view (MUSM 2598; CTA-44). AM: Chiroptera: unidentified emballonurid, right lower canine in lingual view (MUSM 2599; CTA-75). Scale bars = 100 µm (A-G), 200 µm (H-I), 0.5 mm (O, AF), 1 mm (L, X-Z, AE, AG, AM), 2 mm (J, P-Q, AA-AB, AJ-AK), 5 mm (K, M-N, W, AH-AI, AL), 10 mm (R-V, AC-AD).

Fig. 11. Taxonomic diversity as depicted in the Contamana section throughout the Eocene-Miocene interval, excluding palynomorphs. A: Overall taxonomic diversity at the order, family, and species levels within documented classes. Evolution of taxonomic diversity through time, at the (B) class, (C) order, (D) family, and (E) species levels. Time intervals considered coincide with standard ages of fossil-yielding localities: ME, Middle Eocene; LE, Late Eocene (not documented); EO, Early Oligocene (not documented); LO, Late Oligocene; EM, Early Miocene; MM, Middle Miocene; LM, Late Miocene. The early Paleocene interval is not shown. In all diagrams (A-E), taxa listed in the box (top right) appear clockwise. See Supplementary Data for further details.

Fig. 12. Chronostratigraphic diagram of Cenozoic deposits in the Ucayali basin, with comparison to the northern and southern Peruvian foreland basins. Based on data from Kummel (1948), Roddaz et al. (2010), Marivaux et al. (2012), Antoine et al. (2013), Louterbach et al. (2014), Boonstra et al. (2015), Eude et al. (2015), references therein, and our own observations.

Table captions

Table 1

Location of Cenozoic fossil-yielding localities and other outcrops of interest nearby Contamana, Peruvian Amazonia.

Table 2

Stratigraphic and temporal distribution of charophyte taxa recognized in the Paleogene of Contamana (Huchpayacu and Pozo Fms.), Peruvian Amazonia.

Figure 1

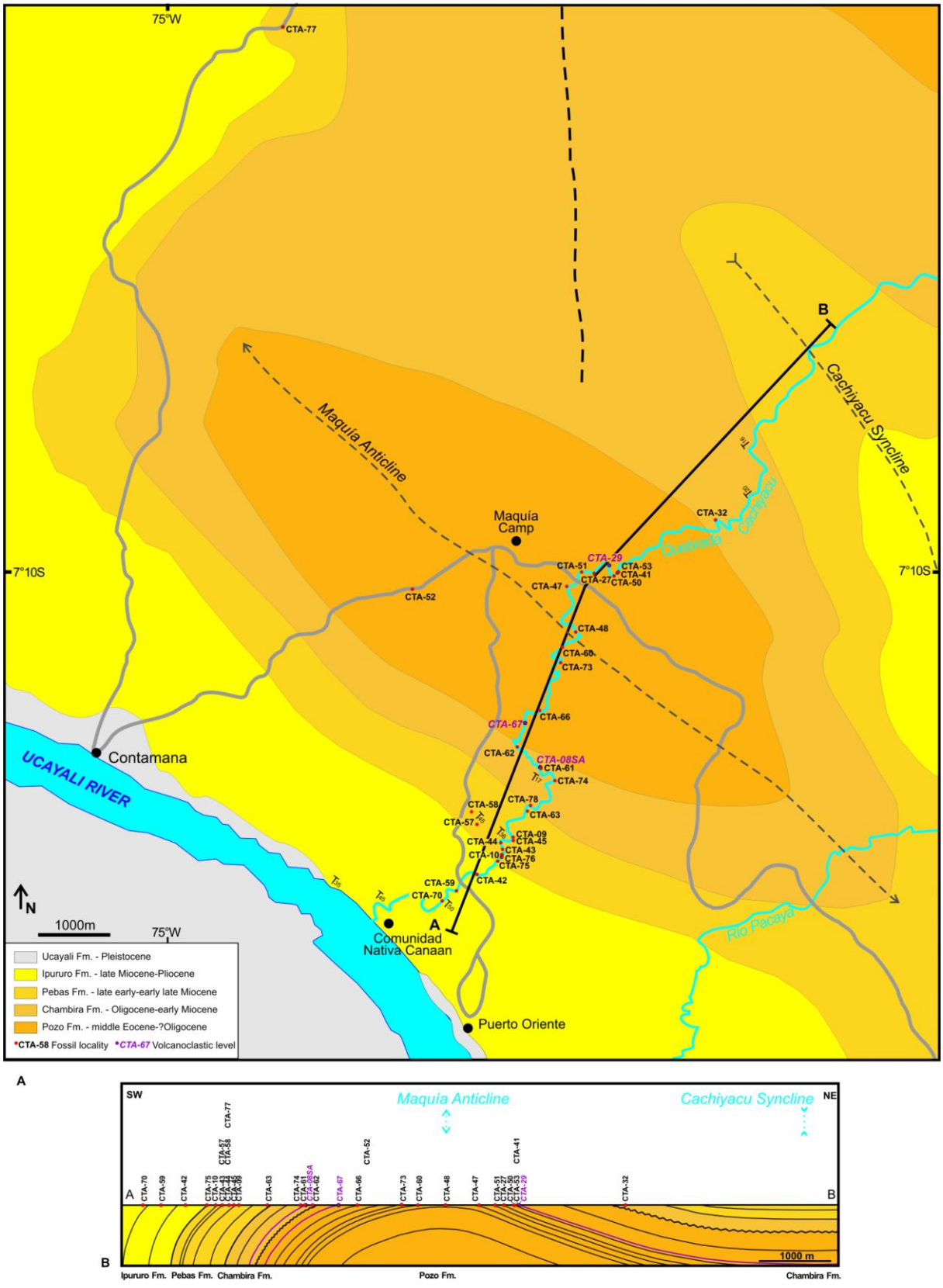


Figure 2

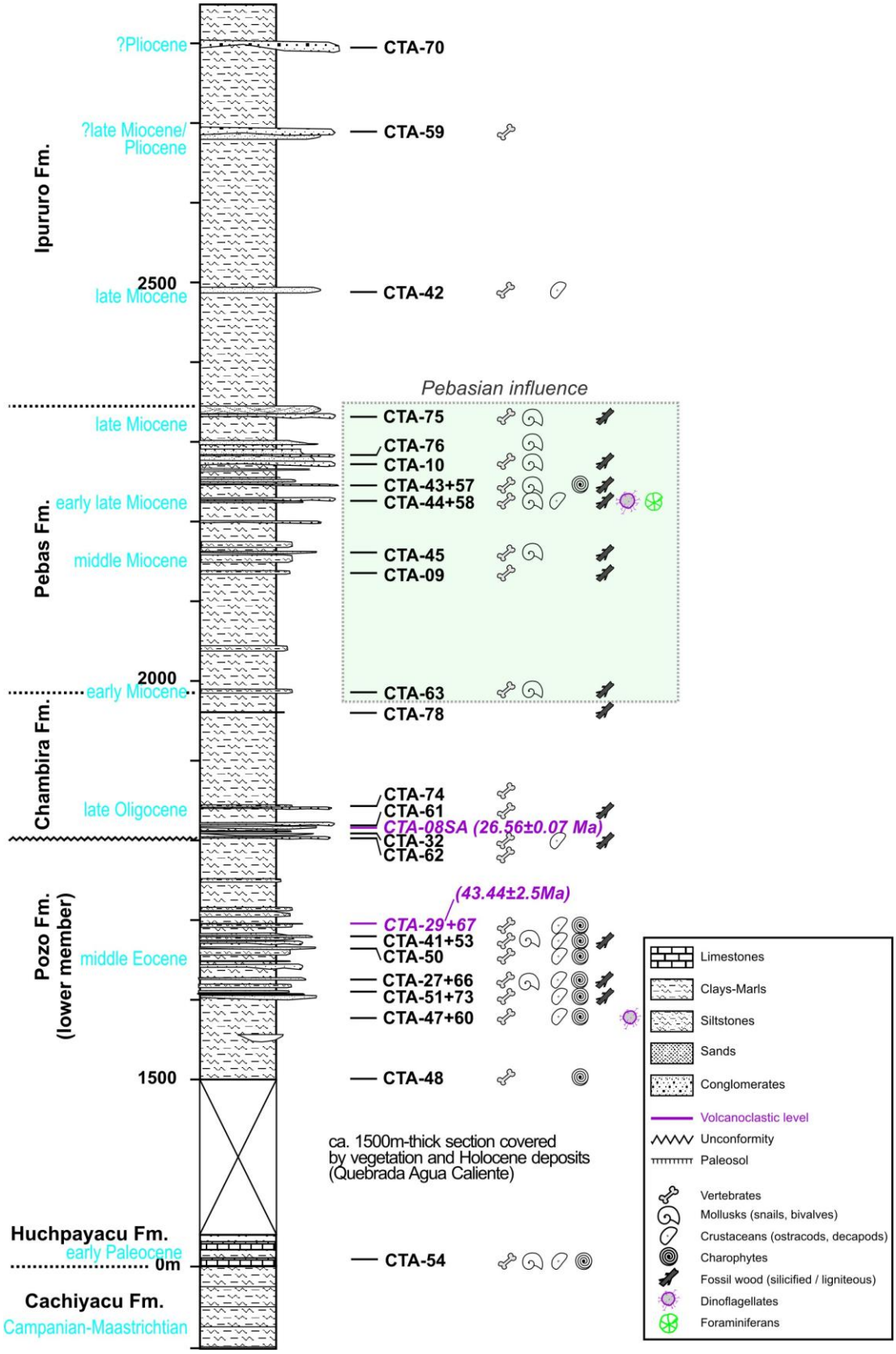


Figure 3

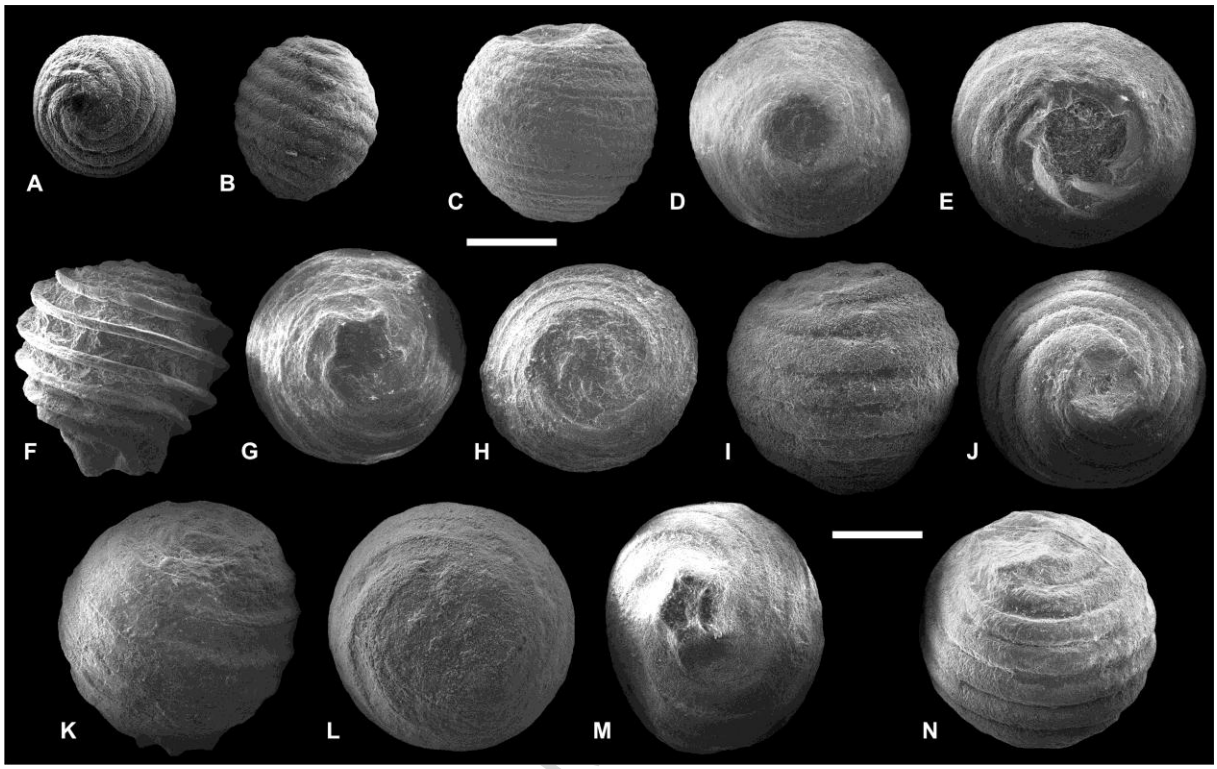


Figure 4

Figure 5

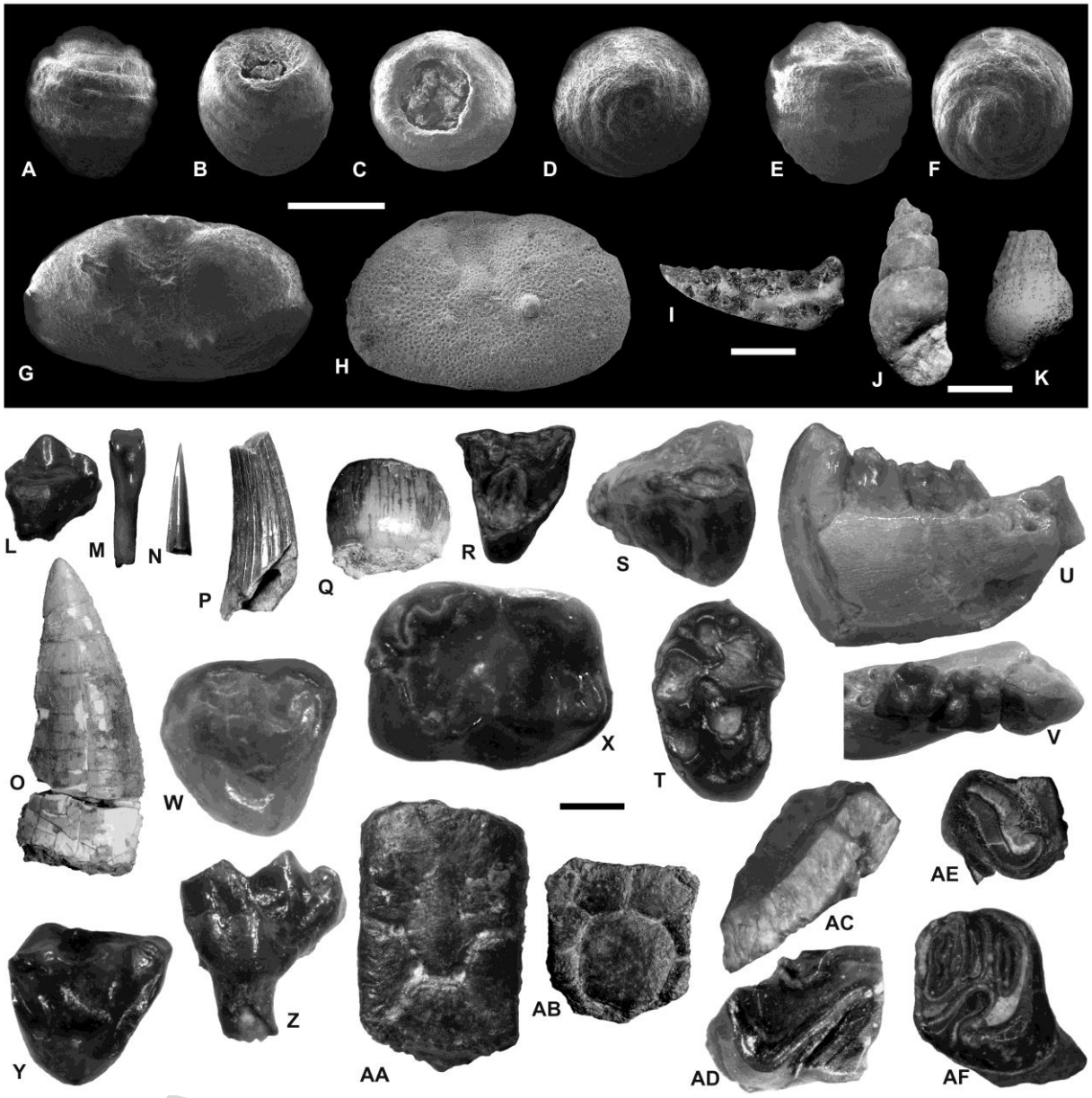


Figure 6

Figure 7

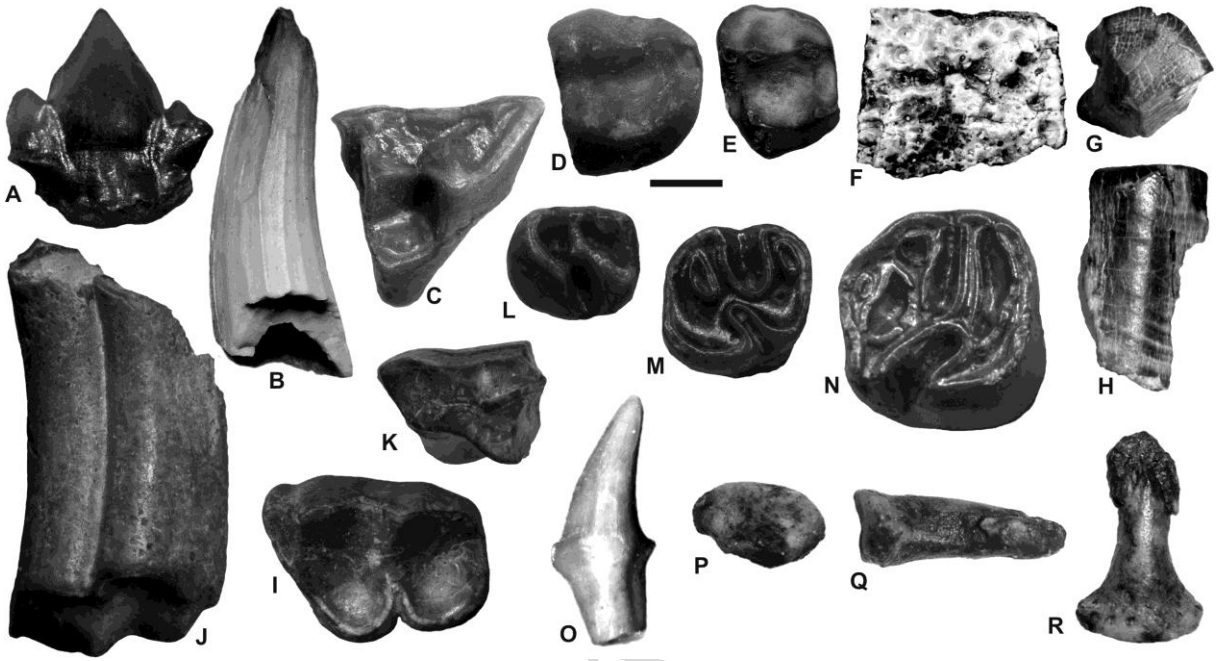


Figure 8

Figure 9

Figure 10

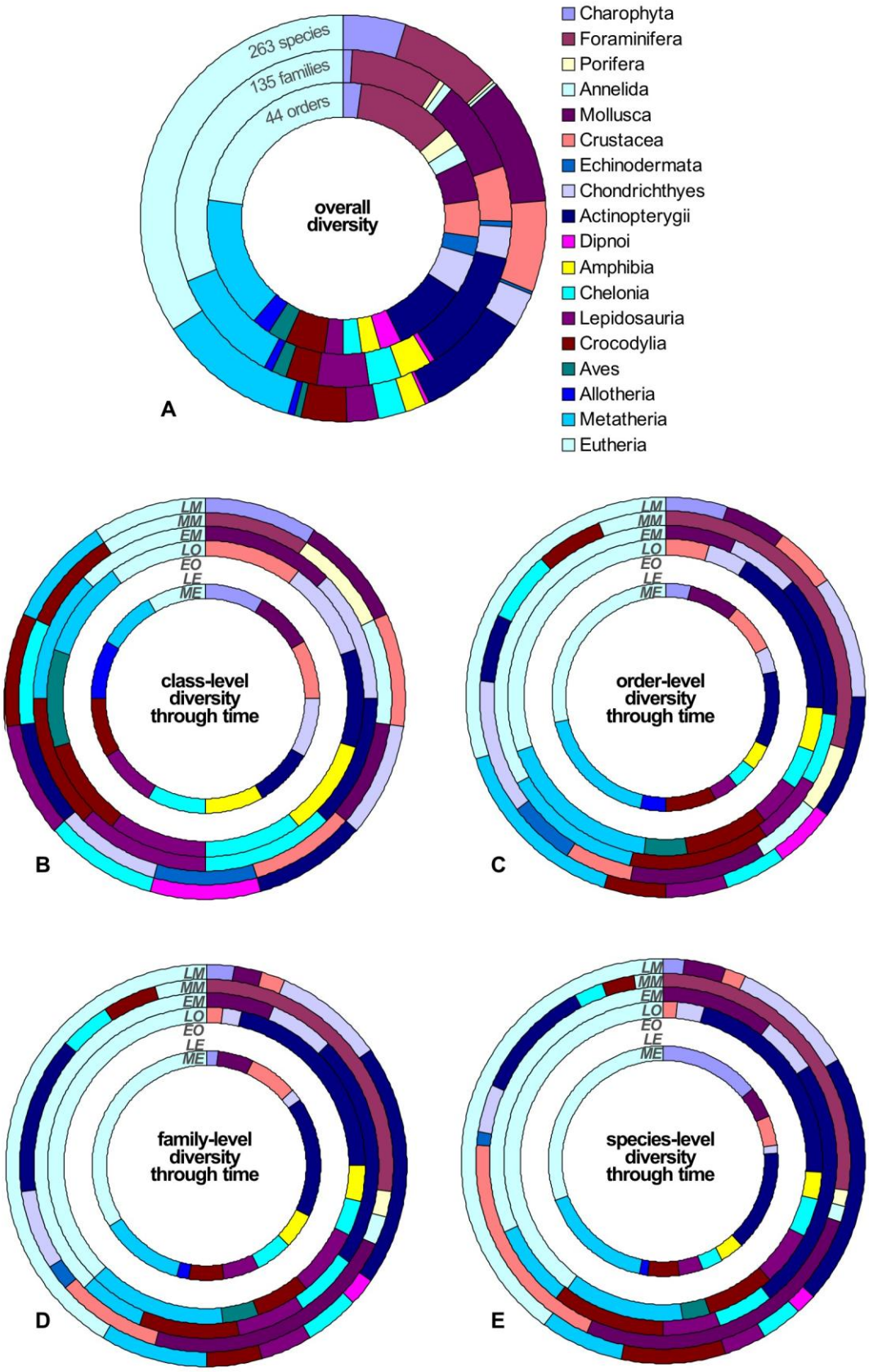


Figure 11

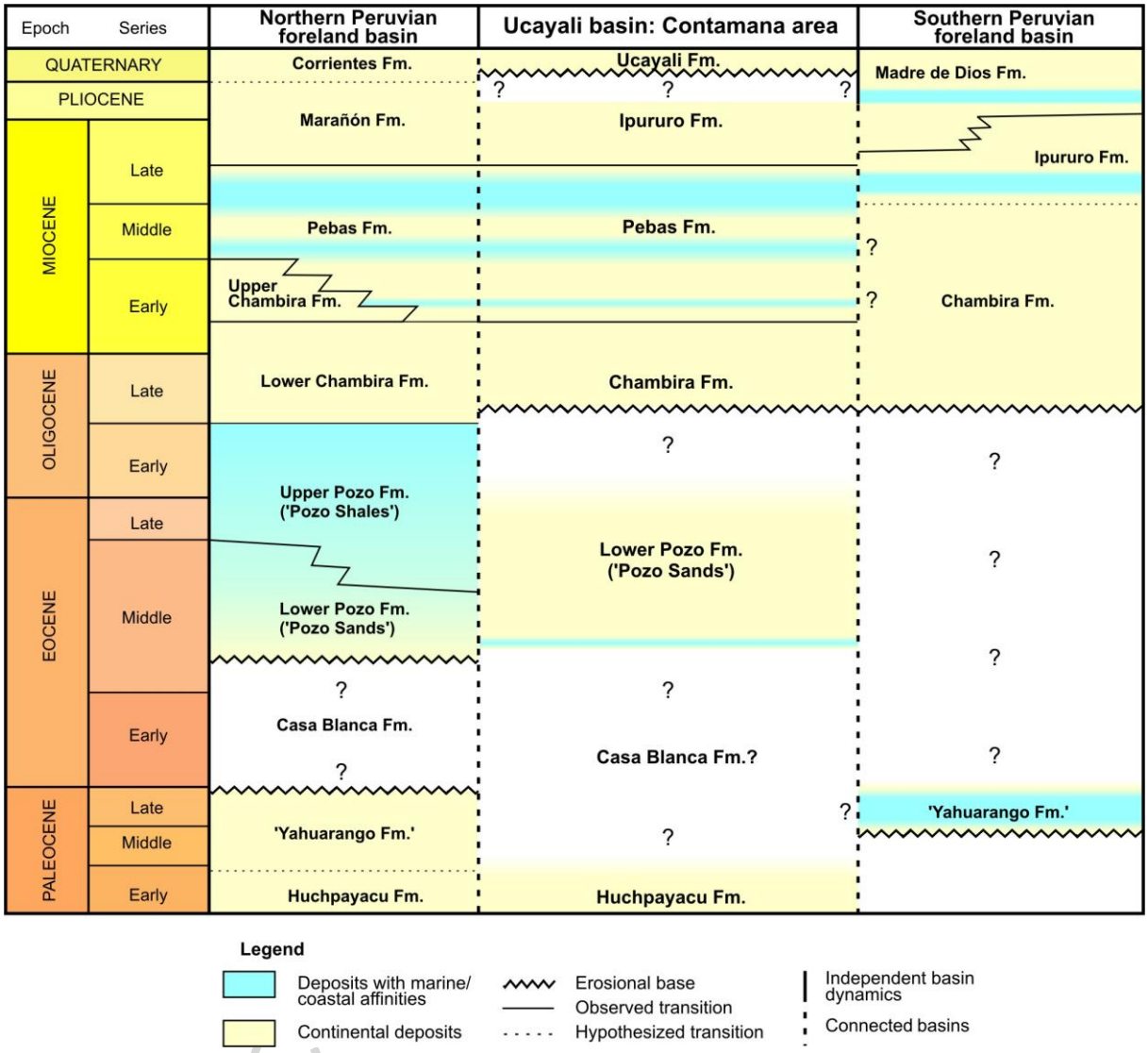


Figure 12

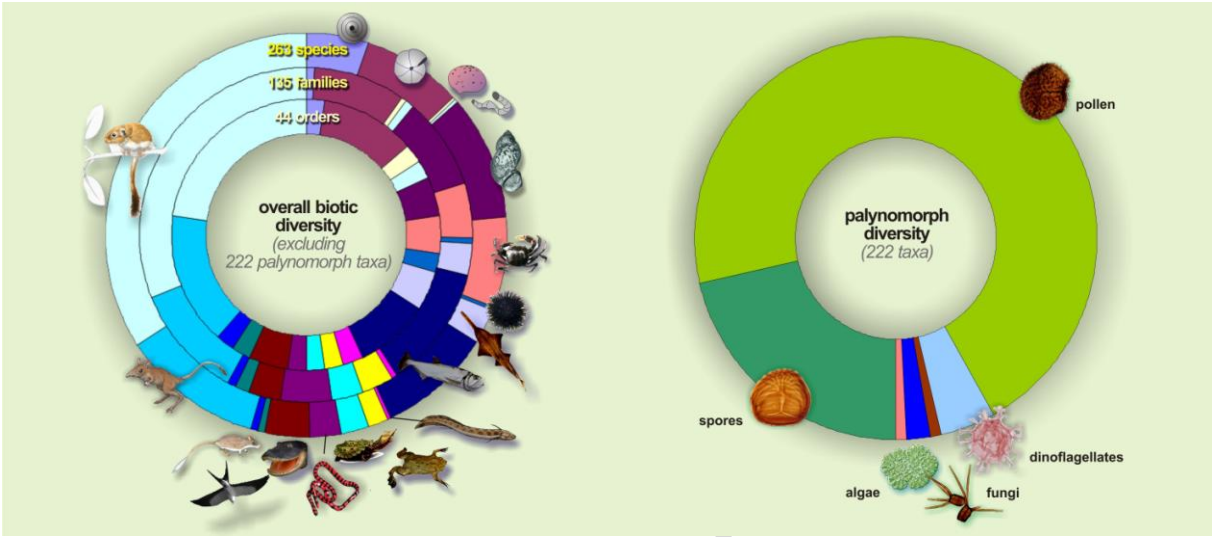
Table 1

Locality	Lat. (S)	Long. (W)	Formation, Member	Hypothesized/constrained age	Depositional environment
CTA-08SA	7.35421	74.95375	Chambira	26.56±0.07 Ma (U/Pb on zircons)	distal ash, fluvial setting
CTA-09	7.36361	74.95708	Pebas	late early-early middle Miocene	fluvial setting
CTA-10	7.36538	74.95812	Pebas	late Miocene	fluvial setting
CTA-27	7.33011	74.94733	Pozo, lower member	late middle Eocene	fluvial setting
CTA-29	7.32859	74.94556	Pozo, lower member	late middle Eocene	fluvial setting
CTA-32	7.32374	74.93284	Chambira, base	late Oligocene	oxbow lake
CTA-41	7.32923	74.94468	Pozo, lower member	late middle Eocene	fluvial setting
CTA-42	7.36743	74.96035	Ipururo	late Miocene-Pliocene	fluvial setting
CTA-43	7.36497	74.95793	Pebas	earliest late Miocene (Mayoan)	tidal interface
CTA-44	7.36415	74.95833	Pebas	middle-late Miocene transition	coastal channel, marine influence
CTA-45	7.36388	74.95708	Pebas	middle Miocene	coastal channel, tidal influence
CTA-47	7.33113	74.95127	Pozo, lower member	middle Eocene	fluvial setting, marine influence
CTA-48	7.33632	74.95067	Pozo, lower member	middle Eocene	floodplain
CTA-49	7.33522	74.95158	Pozo, lower member	middle Eocene	floodplain
CTA-50	7.32957	74.94492	Pozo, lower member	late middle Eocene	fluvial setting
CTA-51	7.32948	74.9492	Pozo, lower member	late middle Eocene	fluvial setting
CTA-52	7.33193	74.9707	Pozo, lower member	late middle Eocene	floodplain
CTA-53	7.32921	74.94461	Pozo, lower member	late middle Eocene	fluvial setting
CTA-54	7.2147	74.94937	Huchpayacu, lower member	Paleocene	lacustrine setting
CTA-57	7.36191	74.96111	Pebas	earliest late Miocene (Mayoan)	oxbow lake
CTA-58	7.36004	74.96223	Pebas	middle-late Miocene transition	marine setting/mangrove
CTA-59	7.36878	74.96551	Ipururo	latest Miocene-Pliocene	fluvial setting
CTA-60	7.33964	74.95255	Pozo, lower member	middle Eocene	fluvial setting
CTA-61	7.35448	74.95366	Chambira, base	late Oligocene	fluvial setting
CTA-62	7.35335	74.95573	Chambira, base	late Oligocene	fluvial setting
CTA-63	7.36053	74.95551	Pebas, base	early Miocene (Colhuehuapian)	lacustrine setting, marine influence
CTA-65	7.32893	74.94551	Pozo, lower member	late middle Eocene	fluvial setting
CTA-66	7.34876	74.95431	Pozo, lower member	late middle Eocene	fluvial setting
CTA-67	7.35015	74.95563	Yahuarango top	late middle Eocene	distal ash, fluvial setting
CTA-72	7.25116	74.97200	Chambira/Pebas	late Oligocene-early Miocene?	floodplain
CTA-73	7.34160	74.95241	Pozo, lower member	late middle Eocene	fluvial setting
CTA-74	7.35618	74.95241	Chambira	late Oligocene	fluvial setting
CTA-75	7.36596	74.95855	Pebas, top	late Miocene (Mayoan-Chasicoan)	fluvial setting
CTA-76	7.36553	74.95818	Pebas	late Miocene	estuarine embayment
CTA-77	7.25229	74.97757	Pebas	middle-late Miocene transition	marine setting/mangrove
CTA-78	7.35988	74.95498	Chambira top	?early Miocene	floodplain deposit, terra firme

SYNCL-CACH	7.30093	74.92073	?Pebas	?Miocene	fluvial setting

Table 2

Taxon name	Localities / number of specimens									Stratigraphic Range (and references)
	CTA-54	CTA-47	CTA-51	CTA-73	CTA-27	CTA-66	CTA-50	CTA-41+53	CTA-29	
Chara "*Grambastichara*" *subcylindrica*	15									Paleocene-early Eocene; Mourier et al., 1988
Sphaerochara inconspicua	13									Cretaceous-Paleocene; Feist & Brouwers, 1990
Sphaerochara huaroensis	19									early Paleocene; Jaillard et al., 1994
Nitellopsis supraplana sulcata	12									Paleocene-early Eocene; Mourier et al., 1988
Peckisphaera cf. *portezueloensis* - *Peckichara* sp.	11									latest Cretaceous; Chassagne-Chassagne-Manoukian et al., 2013
Pseudolatochara sp.	16									Cretaceous-Eocene; Vialle et al., 2013
Nitellopsis (*Tectochara*) *merianii*	14									panchronic
Peckichara cf. *varians*	2									Paleocene; Musacchio, 2006
Chara? sp.	20									panchronic
Lamprothamnium sp.?	20									Paleocene; Musacchio, 2006
Brevichara sp.?	4									panchronic
Platychara cf. *perlata*?	5									late Cretaceous-early Paleocene; Louterbach et al., 2014
Peckichara sp.?	3									late Cretaceous-Paleocene; Mebrouk et al., 2009
Charales indet.	30	4								panchronic
Raskyella pecki meridionale		5	4		3	2	30	41	15	Eocene; Martín-Closas & Guerrero, 2005
Nodosochara jorbae		4								Eocene; Adaci et al., 2007; Sanjuan & Martín-Closas, 2014
Pseudolatochara sp.? – *Latochara* sp.?		3								Paleocene-Eocene; Vialle el al., 2013
Lamprothamnium stipitatum			6							panchronic
Nitellopsis (*Tectochara*) *latispira*				2						late Eocene-early Oligocene; Sanjuan & Martín-Closas, 2014
Chara (*Grambastichara*) *tornata*				10						panchronic
Psilochara sp.				6		2				panchronic
Stephanochara acris					4					Ypresian; Adaci et al., 2007
Lychnothamnus major						1				early Oligocene; San Juan & Martín-Closas, 2014
Lychnothamnus (*Pseudoharrisichara*) *tenuis*						1				Santonian-Campanian; Musacchio, 2010
Lychnothamnus sp.?						2	4			panchronic
Total number of specimens	184	16	10	18	7	6	34	41	15	



Graphical abstract

Research Highlights

We report 485 fossil species (Paleocene–?Pliocene) in Peruvian Amazonia

The Paleogene interval has higher levels of biotic diversity than the Neogene

Peruvian Amazonia experienced two marine pulses ~43 and ~12 million years ago